Biology of Caviomorph Rodents:
Diversity and Evolution

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SAREM Series A
Mammalogical Research
Investigaciones Mastozoológicas

SAREM Series A
Mammalogical Research
Investigaciones Mastozoológicas
Buenos Aires, Argentina
ISBN: 9789879849736

SAREM - Sociedad Argentina para el Estudio de los Mamíferos
Av. Ruiz Leal s/n, Parque General San Martín. CP 5500, Mendoza, Argentina
http://www.sarem.org.ar/

Cover photograph: *Dolichotis patagonum*
Credits: Cecilia C. Morgan

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In 2013, during the Annual Assembly of SAREM in the city of Mar del Plata, Dr. Mariano Merino, then President of the Society, together with the rest of the Directive Committee, announced the launch of a new editorial Project: **SAREM Series A: Mammalogical Research (Investigaciones Mastozoológicas).** The goal of this publication was to be the dissemination of scientific works on Neotropical mammals from wide and varied perspectives (evolutionary history, systematics, paleontology, biogeography, morphology, ecology, physiology, etology, conservation, genetics, etc.) aimed at a public formed by the mammalogy research community, graduates, students and other interested readers, at both national and international levels.

With this first book, *Biology of Caviomorph Rodents: Diversity and Evolution*, SAREM inaugurates the publication of novel works of a different nature compared to those already published in the journal Mastozoología Neotropical (Neotropical Mammalogy). In this series, each volumen will be dedicated to a specific subject, be it a particular taxon (*e.g.*, taxonomy of caviomorphs, marsupials, carnivores, primates, etc.) or discipline (*e.g.,* ecology of small mammals, conservation, etc.). This series is meant to allow publication of unpublished works and revisions resulting from scientific meetings, symposia or workshops, so that they may achieve wide distribution in the international scientific community.

It is our hope that this new series becomes a tool for further development of studies of mammals, one that can be used by the mammalogical community with the unwavering purpose of promoting the knowledge and dissemination of mammalogy in South America.

Dr. Emma Carolina Vieytes
Editor-in-Chief SAREM Series A

Dr. David Alfredo Flores
President SAREM

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Foreword

The Caviomorpha is the most diverse clade of rodents when viewed by overall bauplan, and is by far the most species rich among any of its fellowhystricomorphous or hystricognathous cousins. No other group of rodents, or other mammalian lineage, can boast the body size diversity exhibited by caviomorphs through time –one covering five orders of magnitude, from ~100 g in the living octodontid *Spalacopus* to nearly a metric ton in the extinct dinomyid †*Josephoartigasia*. Nor does any other rodent group encompass the array of social and mating systems ofextant caviomorphs. Confined to the Neotropical Realm (with the single exception of the Nearctic porcupine, *Erethizon*), and distributed across every terrestrial biome from sealevel to well above treeline in the high Andes, and from rainforest to desert, the Caviomorpha is also among the oldest of all rodent groups,one represented byperhaps the best fossil record of any.

This wonderfully disparate assemblage is brought to life through the chapters in this volume, contributions by scholars who know these animals intimately, and from long personal experience in the field and/or in the laboratory. All have spent decadespicking fossils from matrix, handling live animals caught in traps, measuring physiological parameters, making direct or indirect observations, or examining specimens in the museum. As editors Vassallo and Antenucci note in their Introduction, this volume was conceived as "a new synthesis or integration ... made from different disciplines." As promised, both the individual and combined chapters do, indeed, provide the key overviews of current knowledge while also offering new insights into evolutionary history and diversification. In doing so, this volume constructsthe platform upon which the next generation of studies can, and will, be built.

My own introduction to the Caviomorpha began in graduate school when I took a seminar from George Gaylord Simpson, doyen of mammalian paleontology and anadvocate of "sweepstakes routes" and "waif dispersal" as fundamental principlesunderlying biogeographic pattern. This course coincided, in the mid-1960s, with the discovery of sea-floor spreading and, through a developing understanding of global plate tectonics, the re-wakening of Alfred Wegener's long discounted theory of continental drift. Today, one cannot doubt but that caviomorph entry into South America, from Africa, was promoted by plate dynamics, or that their subsequent diversification elegantly illustrates the "splendid isolation" of that continent championed by Simpson. At the very end of my graduate studies, I had the chance to experience caviormorph diversity first-hand in the eastern lowlands of Peru. Here I had my initial encounter with rainforest taxa like prehensile-tailed porcupines, pacas, agoutis, acouchis, and especially the bewildering diversity of spiny rats. It was also herewhere I became mesmerized by the staccato calls of bamboo rats at night along the river. My experiences with caviormorphs expanded in subsequent decades, during fieldwork centered in Amazonia but also ranging from the Patagonian steppe and *Nothofagus* forests of southern Argentina, through the Altiplano of Peru, and into the Atlantic Forest and Cerrado of Brazil. Much of my research passion over these decades, begun with that first experience in Peru, remained focused on diversification pattern and process among the highly speciose Echimyidae.

In their introduction, Vassallo and Antenucci detail the focus and primary coverage of each of the 10 contributions that follow. To their words, I offer a few of my own.

Vucetich and her co-authors, in Chapter 1, describe the tempo and mode of the fossil history of caviomorphs, and in so doing provide the critical backdrop to the queries of all interested in caviomorph diversity, no matter thespecific discipline. Many will immediately recognize the categorical placement of some of the superbly preserved skulls and teeth that are illustrated, or will otherwise marvel over those not so clearly recognizable. These authors importantly, and clearly, point to connections between fossil lineages and extant taxa, but also identify those either suspect or without an as yet firm understanding. While reading this contribution, I was reminded what my friend and Berkeley colleague, the late Vincent Sarich, often stated. Vince was one of the first molecular phylogeneticists to reconstruct rodent phylogeny, including that of caviomorphs. In discussions of the often-observedconflict between relationships posited from the fossil record and the molecular trees then being drawn, Vince would remind one, with his usual forceful candor: "we are certain that molecules had ancestors, but we can only hope that fossils had descendants." As Vucetich *et al.* demonstrate, many of the fossil taxa now known during the long and rich history of caviomorphs in South American clearly did leave off spring.

Both Upham and Patterson (Chapter 2) and Ojeda and colleagues (Chapter 3) illustrate the geographic pattern of extant taxon density, overall centered in the humid Amazonian and Atlantic forests but with each major clade exhibiting its own unique distribution pattern. While the former largely focuses on the timing and pattern of lineage diversification, the latter dissects current functional ecology, from range sizes and substrates to feeding niches. Rocha-Barbosa *et al.* (Chapter 4) and Morgan (Chapter 5) expand on Ojeda et alia's ecological perspective by incorporating, respectively, an ecomorphological locomotory axis and a functional shape analysis of postcranial elements to caviomorph diversification, the first noting in particular the numerous parallels with various small-bodied cervoid or bovoid lineages in paleo-tropical systems. And Álvarez and colleagues (Chapter 6) examine the primacy of a food axis through the combinatory lens of incisor structure, cheektooth specialization, and the craniomandibular masticatory apparatus, also employing a functional biomechanical approach and emphasizing constraint and opportunity driven by diversity in habitusand social system.

These first six chapters cover evolutionary history, phyletic relationships, and diversification, in bothecological and functional character contexts. The last four chapters zero in on the"non hard part" components of the living animals. These include social system (Herrera, Chapter 7) and energetics (Luna *et al*., Chapter 8), both as sets of adaptations importantly placed in the context of costs relative to diet, habitat, and sociality. MacManes *et al*. (Chapter 9) tie population parameters, like demography and demographic history, to social system ecology as well as to population genetic diversity in functional gene complexes, such as the MHC system. They show how high-throughput sequencing technology will revolutionize our ability to uncover the genetic basis of behavioral and/or ecological differences and commonalities, be these allelic changes in structural genes or those involving upstream or downstream regulation that underlietiming shifts in gene expression. While not explicitly covered, these same technologies will be equally critical in elucidating the genetic basis of functional-morphological adaptations, such as tooth crown height and occlusal surface changes, thus tying explicit genes and their control to the key innovations that drove caviomorph diversification.

Most of the chapters in the book are introspective, in that each focuses on diversity and disparity within the caviormoph lineage itself. The final contribution, that of Zapata and colleagues (Chapter 10), however, views caviomorphs vis-a-vis their pivotal role in structuring the communities in which they exist, in this case by regulating and sustaining the ecological diversity of their predators.We learn, for example, how caviomorph species in local communities not only support a diverse predator base but alsoinfluence trophic guildstructure. These observations, combined with those developed especially in Chapter 3, show how caviomorphs have both top-down and bottom-up influences on the larger communities, biotic and abiotic, in which they are members.

My own area of expertise is in systematics, which I define following G.G. Simpson as "the study of the diversity of life," a broadened view that provides the conceptual framework binding this volume together. I thus end by emphasizing two essential elements of Upham and Patterson's expansive presentation of caviomorph molecular phylogenetics. First, their analysis covers almost all extant genera for the first time, including those largely known only from a few, long-ago collected museum specimens. Their phyletic hypotheses will serve as the baseline for all future studies where phylogenetic inference is essential, even if not all nodes in the caviomorph tree are as yet firmly established. And, I especially encourage those who wish to unravel the diversification history of any and all modern South American groups, be these mammal or not, to reflect on Fig. 6 and the accompanying text, which integrate available information on the tectonic, landscape, and climate histories of South America from the Eocene to the present. Even if there remains much to understand of these separate histories, we should all remember that associations of taxa with the biomes of today, includingboth current composition and geographic placement, must be viewed within the context of a dynamic history involving many axes rather than through the myopic view of a single history static overboth time and space.

This is a rich volume, with state-of-the-art data presentations and analyses, and both thorough and substantive summaries of current knowledge. In its scope and coverage, therefore, this treatise truly does justice to the exceptionally diverse group that is the Caviomorpha.

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1 | A BRIEF HISTORY OF CAVIOMORPH RODENTS AS TOLD BY THE FOSSIL RECORD

BREVE HISTORIA DE LOS ROEDORES CAVIOMORFOS SEGÚN EL REGISTRO FÓSIL

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Abstract. Caviomorph rodents have a very rich fossil record that provided good bases for understanding the major pathways of their evolution, at least in southern South America. The evolution of caviomorphs in intertropical South America is less known, although the knowledge of the Quaternary record has been improved in recent years. In this chapter we analyze this record and describe the most important features of their evolutionary history. The caviomorph ancestors probably entered South America during the middle Eocene by rafting from Africa, and the first steps of their evolution occurred in intertropical areas. The evidence strongly suggests that the initial radiation of caviomorphs was more complex than hitherto postulated, with the differentiation of some taxa that cannot be assigned to any of the major clades in which caviomorphs are classically divided (the superfamilies Octodontoidea, Erethizontoidea, Cavioidea, and Chinchilloidea). Caviomorphs arrived in Patagonia during the latest Eocene or early Oligocene, and by the late Oligocene they were highly diversified, with representatives of the four main lineages. A great morphological disparity, at least in tooth morphology, was then acquired mainly by the development of hypsodonty in several lineages. The early evolution of each of the major clades was also more complex than previously proposed, especially for chinchilloids and octodontoids. The first stages of the evolution of cavioids are more obscure because they are recognized through the relatively derived Deseadan species of Cavioidea *s.s*. Moreover, the steps that led to the differentiation of Dasyproctidae, Cuniculidae and some Oligocene - Miocene forms (*e.g.*, *Neoreomys*), are not known or not well understood yet. One of the most outstanding features of caviomorphs, the development of large size, appears as a complex phenomenon. Large size evolved independently in multiple lines, in what looks to be a coeval coordinated phenomenon.

Resumen. Los roedores caviomorfos poseen un registro paleontológico muy rico que permite establecer los patrones generales de su historia evolutiva, al menos para la parte austral de América del Sur (aproximadamente equivalente a la Subregión Patagónica de Hershkovitz, 1958). El registro de la región intertropical (aproximadamente equivalente a la Subregión Brasílica de Hershkovitz, 1958) es mucho más escaso y solo permite una visión muy limitada sobre la evolución del grupo en esta región, aunque el registro Cuaternario especialmente de Brasil se ha incrementado mucho recientemente. En este capí-

tulo analizamos el registro y describimos los rasgos más importantes de la historia evolutiva del grupo. Los caviomorfos habrían llegado a América del Sur durante el Eoceno medio desde África por medio de balsas naturales. Las primeras etapas de su evolución se habrían desarrollado en la región intertropical. Las evidencias disponibles hasta ahora, tanto provenientes del registro como de análisis filogenéticos con datos morfológicos indican que esta etapa habría sido más compleja de lo supuesto hasta ahora. Los nuevos aportes muestran que se habrían diferenciado taxones que no pueden ser clasificados en ninguno de los clados principales en que clásicamente se ha dividido a los caviomorfos (las superfamilias Octodontoidea, Erethizontoidea, Cavioidea y Chinchilloidea). La evolución temprana de cada uno de estos linajes principales también habría sido muy compleja, al menos para los chinchilloideos y octodontoideos. Las primeras etapas en la evolución de Cavioidea son menos conocidas principalmente porque es necesario resolver las afinidades de los taxones del Eoceno medio-Oligoceno temprano (*e.g.*, *Branisamys*, *Andemys*, etc.) propuestos para esta superfamilia. Sin embargo, análisis recientes focalizados en Cavioidea *sensu stricto* muestran una historia evolutiva compleja para este grupo a través de diferentes pulsos de diversificación, lo cual indicaría una diversidad taxonómica mayor de la conocida hasta ahora. Más aún, los pasos que llevaron a la diferenciación de los otros cavioideos (Dasyproctidae, Cuniculidae y otras formas del Oligoceno-Mioceno como *Neoreomys*), son prácticamente desconocidos. Los caviomorfos habrían llegado a latitudes altas (centro de Chile y Patagonia central) hacia el Eoceno tardío u Oligoceno más temprano. Esta migración quizá se haya visto favorecida por el cambio climático del límite Eoceno-Oligoceno que habría permitido el desarrollo de nuevos ambientes. Hacia el Oligoceno tardío (Edad Mamífero –SALMA por sus siglas en inglés– Deseadense) los caviomorfos ya estaban altamente diferenciados y se pueden reconocer claramente los representantes de las cuatro superfamilias. Los roedores deseadenses muestran una segunda etapa de radiación que es a su vez la primera radiación patagónica. En ellos se manifiesta una alta disparidad morfológica al menos a nivel dentario, que demuestra la adaptación a ambientes y dietas muy distintas. Aparecen, por ejemplo, las primeras especies con dientes de crecimiento contínuo. Durante el Mioceno más temprano (SALMAs Colhuehuapense y "Pinturense") se registra una muy alta diversidad con más de 36 especies. Para este período se conoce una gran diversidad de octodontoideos y corresponde, asimismo, al acmé de los puercoespines. Por otra parte, se registran todavía numerosos taxones que retienen caracteres primitivos, como la presencia del premolar deciduo 3 (DP3) en estadios juveniles. Durante el final del Mioceno temprano, representado por la SALMA Santacrucense, se produce un importante cambio con la reducción en diversidad de los pequeños octodontoideos braquiodontes y los puercoespines, pero con la diversificación de formas euhipsodontas de cavioideos y chinchilloideos. Este incremento de taxones euhipsodontes siguió el cambio climático y la subsecuente expansión de los ambientes abiertos. El Mioceno medio es un período relativamente poco representado, pero de singular importancia en la evolución de los caviomorfos ya que implica una modernización del grupo: se extinguen numerosos linajes antiguos, pero se desarrollan muchos linajes (familias y subfamilias) que tienen representantes vivientes como Caviinae, Dolichotinae e Hydrochoerinae. El Mioceno tardío (SALMAs Chasiquense y Huayqueriense) está muy bien representado en Argentina central y norte. Muchos linajes modernos tienen su primer registro o se hacen abundantes en este lapso. Los octodontoideos se hacen muy abundantes y diversos, representados por taxones claramente asociados a linajes con representantes vivientes, como el equímido *Theridomysops* estrechamente relacionado a *Clyomys* y *Euryzygomatomys*, o *Protabrocoma*, estrechamente relacionado a *Abrocoma*. Los octodóntidos y los hidroquerinos en particular son muy diversos. Un rasgo muy destacado es el registro detallado de etapas sucesivas en la adquisición de la hipsodoncia en varios linajes de octodontoideos provenientes de la Formación Cerro Azul en la provincia de La Pampa. Este es uno de los mejores ejemplos del desarrollo de la hipsodoncia en el que se observa claramente el cambio morfológico y la

modificación del *schmelzmuster* (distribución espacial de los tipos de esmalte) asociado al progresivo aumento de la altura de la corona. Se registra en este período el acmé de los dinómidos y es también el comienzo del período de gigantismo en los caviomorfos. Durante el Plioceno los caviomorfos del centro de Argentina experimentaron un fuerte empobrecimiento dado por la reducción en diversidad de los Dinomyidae y la extinción local de "Echimyidae" y Erethizontidae y la extinción de los Neoepiblemidae. Este cambio fue probablemente inducido por cambios climáticos y por el impacto producido por la llegada de los mamíferos holárticos participantes del Gran Intercambio Biótico Americano (GABI por sus siglas en inglés). Durante el Pleistoceno queda establecida la composición taxonómica de las faunas de roedores de Argentina, y solamente se observan fluctuaciones en la distribución geográfica de algunos taxones, en respuesta a las oscilaciones climáticas de los períodos glaciales e interglaciales. El registro intertropical es mucho más pobre, pero muestra el desarrollo de algunos linajes exclusivos de esta área, observado por ejemplo, en la fauna de La Venta, Colombia, referida al Mioceno medio. Asimismo, las faunas cuaternarias de Brasil muestran la supervivencia de linajes ya extintos en latitudes más altas por ejemplo, entre los octodontoideos el extinto *Dicolpomys* y los mismos *Clyomys* y *Euryzygomatomys*, así como los últimos dinómidos probablemente relacionados a los gigantes del Mio-Plioceno. Uno de los rasgos interesantes en la evolución de los caviomorfos es el desarrollo de numerosas formas grandes hasta alcanzar en algunos casos tamaños gigantescos para el Orden Rodentia. Este parece haber sido un fenómeno complejo ya que apareció paralelamente y en forma simultánea en todos los linajes principales.

Introduction

Caviomorphs are part of a rich rodent clade, the Ctenohystrica Houchon *et al.* (2000), differentiated in the early Eocene, which are recorded in Asia, Africa and more marginally in Europe (Houchon and Douzery, 2001; Sallam *et al.*, 2011). Caviomorphs reached South America probably during the middle Eocene perhaps synchronously with platyrrhine primates (Frailey and Campbell, 2004; Poux *et al.*, 2006; Vucetich *et al.*, 2010a; Bertrand *et al.*, 2012; Bond *et al.*, 2015). Since then, caviomorphs became one of the most important South American groups of mammals concerning their richness and diversity, particularly since the Oligocene.

Although some authors questioned the monophyly of caviomorphs (Woods, 1982; Bryant and McKenna, 1995; Candela, 1999; Coster *et al.*, 2010), data provided by molecular and morphological phylogenies support this group as monophyletic (Houchon *et al.*, 2000; Houchon and Douzery, 2001; Fabre *et al.*, 2012; Arnal *et al.*, 2014), and suggest an early? or middle? Eocene age for the moment of their differentiation from their African relatives (Poux *et al.*, 2006; Antoine *et al.*, 2012; Fabre *et al.*, 2012).

Living representatives occupy very different environments, from rain forests to puna deserts, and display a great variety of habits such as fossorial, arboreal, riparian and semiaquatic, and a great morphological disparity (Mares and Ojeda, 1982 ; Patton *et al.*, 2015). Living caviomorphs are grouped without difficulty within the four main clades classically recognized, namely the superfamilies Erethizontoidea (New World porcupines, =Erethizontidae for the purpose of this paper), Cavioidea (cavies, maras, mocos, capybaras and pacas), Octodontoidea (spiny rats, tuco-tucos, degus, coypus, and chinchilla rats), and Chinchilloidea (chinchillas, viscachas,

and pacaranas) (see Simpson, 1945; Upham and Patterson, this volume). Their present distribution matches Hershkovitz's (1958; Fig. 1) main biogeographical subdivisons, with some groups restricted to the Patagonian Subregion (Chinchillidae, Octodontidae, Ctenomyidae, Abrocomidae), and others to the Brazilian Subregion [Dasyproctidae, Dinomyidae, Erethizontidae, and "Echimyidae" (quotation marks for Echimyidae are due to the disparate results of internal relationships in phylogenetic analyses; *e.g.*, Carvalho and Salles, 2004; Arnal *et al.*, 2014; Loss *et al.*, 2014; Verzi *et al.*, 2014; Arnal and Vucetich, in press; Upham and Patterson, this volume)]. But when the extinct taxa are included in the study, this systematic arrangement becomes less clear (Arnal, 2012; Antoine *et al.*, 2012; Arnal *et al.*, 2014; Vucetich *et al.*, 2014c), and the geographic distribution of taxa changes substantially, with almost all of the "Brazilian" lineages (*e.g.*, Erethizontidae, "Echimyidae") being represented up to southern Patagonia.

Some features that differentiate caviomorphs from other rodent clades are the great variety of adaptive types achieved along their history (Mares and Ojeda, 1982), the development of gigantic sizes, and the widespread and repetitive development of hypsodonty. In this chapter, the most important features of their evolution in South America will be analyzed through the evidence provided by the fossil record, with attention to the evolution of size and hypsodonty.

Geographic and temporal context

The Cenozoic South American record of continental mammals has a strong geographical bias. Most mammal-bearing localities are found in the southern half of the continent (approximately corresponding with the Patagonian Subregion *sensu* Hershkovitz, 1958). Moreover, Oligocene-early Miocene faunas come mostly from Patagonia (Fig. 1.1), whereas late Miocene-Pliocene faunas come from central to northern Argentina (Fig. 1.2). In northern South America (approximately coincident with the Brazilian Subregion *sensu* Hershkovitz, 1958; Fig. 1) the record is, in contrast, much poorer. This obviously results in a better knowledge of the evolutionary history of austral groups, and therefore of the differentiation, rhythms of evolution, and modes of adaptation of mammals to increasingly unfavorable climatic conditions throughout the Cenozoic, which is expressed more intensely in the southern part of the continent (Le Roux, 2012). Meanwhile, the paleontological record only gives a hint of the evolution of the rich Neotropical rodent fauna through the record in a few localities, especially in Brazil, Peru, and Colombia (Fig. 1). Thus, the knowledge of the history of the taxa currently living in the Brazilian Subregion has to be analyzed mostly on the basis of neontological data. This bias of the record has been reflected in several papers on the evolution of South American mammals (Pascual *et al.*, 1996; Ortiz-Jaureguizar and Cladera, 2006), and specifically of caviomorphs (Pérez and Pol, 2012). In this contribution, the Miocene-Holocene record of the Brazilian Subregion is described separately.

The temporal calibration of the continental Cenozoic of South America (Fig. 2) follows Dunn *et al.* (2013) for the Paleogene and early Neogene, Fleagle *et al.* (2012) and Deschamps *et al.* (2013 and literature therein) for the late Miocene-Pliocene, and Soibelzon *et al.* (2009) for the Quaternary. For the subdivision of the Cenozoic, here we followed the concept of land mammal ages (in our case, South American land mammal ages, SALMAs). "Land mammal ages subdivide geological epochs by recognizing distinctive assemblages of mammal species, each

of which characterize a certain span of geological time" (Barnosky *et al.*, 2014: 2). Thus, these units are intervals of time as represented by fossils, based on mammalian evolution. In the current practice they are considered as biochronologic units (Woodbourne, 2004; Barnosky *et al.*, 2014).

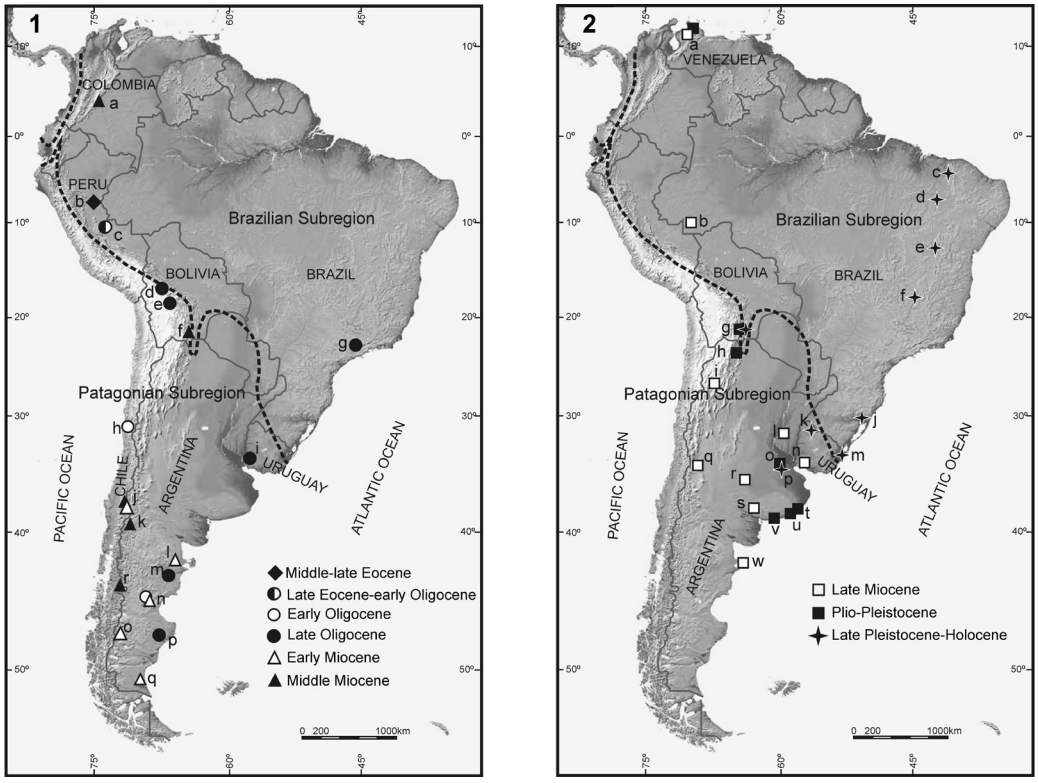


Figure 1. 1. Geographic distribution of most important Eocene-Middle Miocene and 2. Late Miocene-Holocene localities bearing fossil rodents. Dashed line, division between Brazilian and Patagonian subregions (Hershkovitz, 1958). 1. a, La Venta; b, Contamana; c, Santa Rosa; d, Salla-Luribay; e, Lacayani; f, Quebrada Honda; g, Taubaté Basin; h, Tinguiririca; i, Nueva Palmira; j, Laguna del Laja; k, Cañadón del Tordillo; l, Bryn Gwyn; m, Cabeza Blanca; n, Gran Barranca; o, Río Pinturas ; p, La Flecha; q, Río Santa Cruz and coastal area; r, Río Cisnes. 2. a, Urumaco; b, Acre region; c, Ubajara; d, Serra do Capivara; e, Caves of Bahia; f, Lagoa Santa; g, Tarija Valley; h, Uquía; i, Valle de Santa María; j, Río Grande do Sul; k, Sopas Formation, N Uruguay; l, Barrancas del Paraná; m, Chui Creek; n, Barrancas de San Gregorio; o, Toscas del Río de La Plata; p, Río Luján; q, Huayquerías de San Carlos; r, La Pampa (several localities); s, Arroyo Chasicó; t, Chapadmalal area; u, Necochea; v, Monte Hermoso; w, Rincón Chico, Península Valdés.

The fossil record

The oldest records

The oldest caviomorphs come from Peru [Contamana (Antoine *et al.*, 2012) and Santa Rosa (Frailey and Campbell, 2004)], Chile (Tinguiririca; Bertand *et al.*, 2012), and Argentina (La Cantera at Gran Barranca; Vucetich *et al.*, 2010c) (Fig. 1.1). The La Cantera fauna is likely between 30.77 and 30.617 Ma (Dunn *et al.*, 2013), whereas the Tinguiririca fauna is associated with tuffs with 40Ar/39Ar dates of 31.65 ± 0.32 Ma and 31.34 ± 0.17 Ma (Wyss *et al.*, 1993;

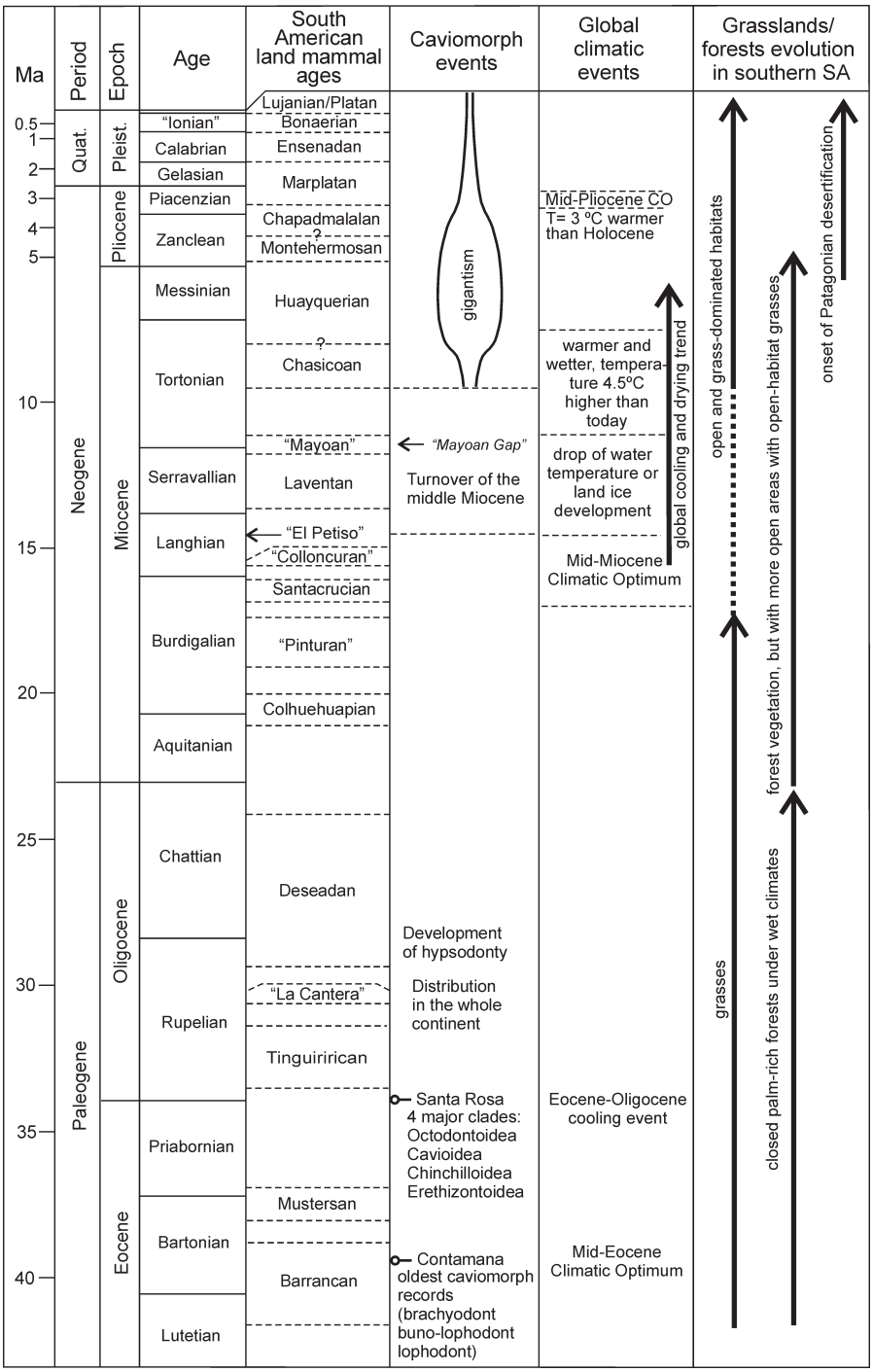


Figure 2. South American Cenozoic temporal calibration and the main events in caviomorph evolution.

Flynn *et al*., 2003, Dunn *et al*., 2013). So, both are likely to be early Oligocene in age and have scant rodent remains (see below).

The fauna from Contamana (locality CTA-27; Figs. 1.1.b, 2), was assigned to the middle Eocene (Antoine *et al*., 2012), on the basis of numerical ages and biochronological data. In association with the rodents there are marsupials, dasypodids, notoungulates, and pyrotheres, known in higher latitudes from the Barrancan-Mustersan SALMAs (Fig. 2). In this locality, cavio-morphs are represented only by isolated teeth, which already display some taxonomic diversity within a relatively low morphological disparity. All the taxa are brachyodont, bunolophodont, or lophodont. Two genera and three species are exclusive to this fauna (*Cachiyacuy contamanensis*, *C. kummeli*, and *Canaanimys maquiensis*; Antoine *et al*., 2012). According to morphological cladistic analyses (Antoine *et al*., 2012; Arnal *et al*., 2014) they are considered as stem caviomorphs. Although these assignments have to be proven by more inclusive phylogenetic analyses, the CTA-27 fauna would already record the first differentiation of at least some of the caviomorph lineages represented today, *e.g*., pan-octodontoids.

The age of the fauna from Santa Rosa (Figs. 1.1.c, 2) is uncertain; lacking numerical ages, it has been referred to the middle Eocene-early Oligocene interval based on its mammal content. The oldest assignments are based especially on the marsupials, but taking together marsupials, cingulates, and notoungulates, a late Eocene-early Oligocene age is suggested (Campbell, 2004; Frailey and Campbell, 2004; Goin and Candela, 2004; Shockey *et al*., 2004; Ciancio *et al*., 2013). The rodent fauna, in particular, is taxonomically very rich, since about 17 species have been recognized. Moreover, Frailey and Campbell (2004) stated that among unstudied material there are other undescribed species. The Santa Rosa rodents were referred to three of the four major caviomorph lineages, Octodontoidea (*e.g*., *Eodelphomys* Frailey and Campbell, 2004), Cavioidea (*e.g*., *Eoincamys* Frailey and Campbell, 2004), and Erethizontoidea (*Eopululo* Frailey and Campbell, 2004), and even to families with modern representatives (Echimyidae, Dasyproctidae, Erethizontidae; App. 1). However, the relationships of the Santa Rosa taxa with the rest of the caviomorphs need further analyses (Vucetich *et al*., 2014c; Arnal and Vucetich, 2014, in press). Concerning its age, two rodent taxa, *Eobranisamys* Frailey and Campbell, 2004 and *Eoespina* Frailey and Campbell, 2004 are probably shared with the Contamana fauna supporting its oldest age. However, one, *Eobranisamys*, could be shared with the fauna of La Cantera, in which case it suggests a younger age. The presence in Santa Rosa of *Eodelphomys* (the largest rodent of this fauna with a simplified occlusal surface) also suggests a younger age, as this taxon is morphologically similar to the Oligocene-early Miocene myocastorines (see below).

The rodents of these two old intertropical faunas are known mostly through isolated teeth, showing a certain morphological monotony compared to those of younger Patagonian and Bolivian faunas (*e.g*., Deseadan). They are all brachyodont (or with an incipient degree of hypsodonty) and bunodont to bunolophodont. This monotony may be interpreted as a result of an evolution within a humid and warm, more or less stable environments. The lack of a more accurate temporal calibration has so far prevented any determination about whether or not this morphological monotony is also influenced by the closeness to the time of their arrival on the continent.

The Oligocene

The Oligocene (Tinguiririan and Deseadan SALMAs plus La Cantera fauna; Figs. 1, 2) has a rich record of caviomorphs showing a greater morphological disparity than older faunas. Representatives of the four superfamilies, with the archetypal dental features that characterize species of the subsequent SALMAs, can be clearly recognized, at least since the Deseadan SALMA. Although a few genera (*e.g.*, *Andemys* Bertrand *et al.*, 2012, *Branisamys* Hoffstetter and Lavocat, 1970) cannot be assigned with certainty to any supra generic taxa (see below).

Octodontoids are the richest and most diverse group (App. 1), including several genera and species. In turn, they represent different lineages (Wood 1949; Wood and Patterson 1959; Patterson and Wood 1982; Arnal *et al.*, 2014; Vucetich *et al*. 2014c, d), which will characterize the rodent faunas of the early and middle Miocene, at least in Patagonia. The Acaremyidae (Wood, 1949; Vucetich and Kramarz, 2003; Arnal and Pérez, 2013; Arnal and Vucetich, 2015; Vucetich *et al.*, 2014d) are likely a group of austral differentiation. The first representatives, the Deseadan *Platypittamys brachyodon* Wood, 1949, *Galileomys baios* Vucetich *et al.*, 2014c (Fig.3.1), and *Changquin woodi* Vucetich *et al.*, 2014d, attest to its differentiation into several lineages (Vucetich *et al.*, 2014c, d). They display a relatively low cheek tooth morphological disparity, as they are brachyodont to protohypsodont forms with different degrees of occlusal simplification within a tetralophodont pattern. They eventually acquired high-crowned cheek teeth and figure-eight occlusal surface, convergent with those of modern Octodontidae (Vucetich and Kramarz, 2003; but see Verzi *et al.*, 2014). The last representative, *Sciamys petisensis* Arnal and Pérez, 2013 persisted until the middle Miocene.

Several taxa from the Oligocene-middle Miocene such as *Ethelomys loomisi* (Wood and Patterson, 1959; Fig. 3.2), *Xylechimys obliquus* Patterson and Pascual, 1968, *Paradelphomys fissus* Patterson and Pascual, 1968, *Adelphomys* Ameghino, 1887a, *Stichomys* Ameghino, 1887a, were referred by Patterson and Pascual (1968) to the Subfamily Adelphomyinae within the Family Echimyidae. A recent cladistic analysis performed by Arnal and Vucetich (in press; Fig. 5) relates these genera to the living *Myocastor coypus*, and, by priority, Myocastorinae (Ameghino, 1902) would be the valid name for this clade (Fig. 5). This group is not related to the living echimyids but represents the sister group of the lineage formed by some living Echimyidae + Octodontidae. Myocastorines (App. 1) are represented in the Deseadan of Patagonia by *Ethelomys loomisi* (Fig. 3.2) and *Xylechimys obliquus*. They are also present in Santa Rosa with *Eodelphomys*. *Prospaniomys priscus* Ameghino, 1902 and *Deseadomys arambourgi* Wood and Patterson, 1959, originally described as echimyids, were since considered as myocastorine and adelphomyine respectively by Patterson and Pascual (1968), but in recent cladistic analyses (Arnal *et al.*, 2014; Arnal and Vucetich, in press) they appeared as a stem octodontoid and an early divergent member of crown Octodontoidea respectively (Fig. 5).

But probably the most interesting taxa of this time are those originally described as octodontoids (the Deseadan *Migraveramus* Patterson and Wood, 1982 and *Sallamys* Hoffstetter and Lavocat, 1970, plus the early Oligocene *Draconomys* Vucetich *et al.*, 2010c) as being small, brachyodont, or slightly hypsodont taxa with bunolophodont cheek teeth. But, according to recent morphological phylogenetic analyses, these taxa are excluded from Octodontoidea (Arnal *et al.*, 2014), or considered stem octodontoids (Arnal and Vucetich, in press). These taxa, together with the recently described *Llitun* Vucetich *et al.*, 2014c (Fig. 3.3) and *Leucokephalos*

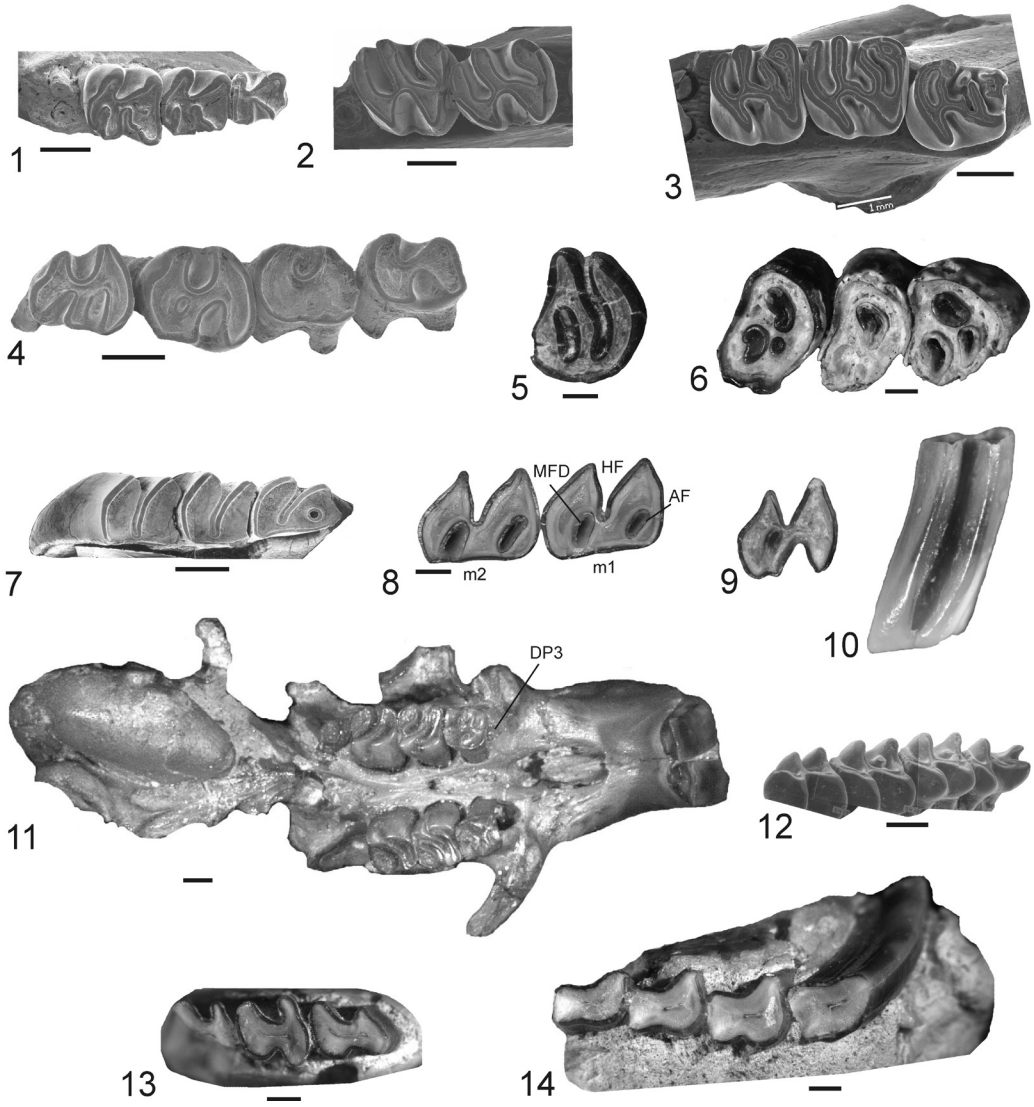


Figure 3. Oligocene-early Miocene caviomorphs. 1. *Galileomys baios* (p4-m3); 2. *Ethelomys loomisi* (m1-m2); 3. *Llitum notuca* (p4-m2); 4. *Leucokephalos zeffiae* (p4-m3); 5. *Incamys meniorum* (M1?); 6. *Leucoreios tretos* (P4-M2); 7. *Eoviscaccia boliviana* (p4-m2); 8. *Chubutomys simpsoni* (m1-m2); 9-10. *Cephalomys cecie* (m1?; 9. occlusal view; 10. external view); 11. *Protadelphomys latus* (skull in ventral view); 12. *Caviocricetus lucasi* (p4-m3); 13-14. *Cephalomyopsis hypselodontus* (13. p4-m2; 14. P4-M3). Anterior to the right. Scale 1 mm. **p**, **P**: lower and upper premolars; **m**, **M**: lower and upper molars.

Vucetich *et al.*, 2014c (Fig. 3.4) form a clade of stem octodontoids with a broad South American distribution that lived during the Oligocene and have no known descendants (Vucetich *et al.* 2014c; Arnal and Vucetich, in press). Thus, the relationships among these taxa, as well as with other caviomorphs, remain controversial.

Chinchilloids are represented by several genera, *Scotamys* Loomis, 1914; *Incamys* Hoffstetter and Lavocat, 1970 (see Vucetich *et al.*, 2014c; Fig. 3.5), *Eoviscaccia* Vucetich, 1989 (Fig.

3.7), and *Loncolicu* Vucetich *et al*., 2014c, probably representing different lineages. *Incamys* and *Loncolicu* retain more generalized dental characters (*e.g*., retention of fossetids on cheek teeth) than the oldest chinchilloid, the Tinguiririan *Eoviscaccia frasinetti* Bertand *et al*., 2012, and they might represent basal chinchillids (Kramarz *et al*., 2013; Fig. 6.2). *Incamys* was originally considered a dasyproctid (Lavocat, 1976), but currently, it is considered to be a probable chinchilloid (Vucetich *et al*., 2014c). Generalized lineages such as that represented by *Loncolicu* may have persisted until the Colhuehuapian as *Garridomys* Kramarz *et al.* (2013), as they share some morphological similarities. *Scotamys* has been interpreted as a possible ancestor of the Chinchillidae *Prolagostomus* and *Pliolagostomus* (Wood and Patterson, 1959) or related to the gigantic neoepiblemids of the late Miocene (Bondesio *et al*., 1975; Kramarz, 2002). *Eoviscaccia*, with several proto- to euhypsodont (*sensu* Mones, 1982) species, is the taxon most clearly related to the living Chinchillidae (*Chinchilla*, *Lagidium* and *Lagostomus*) as demonstrated by Kramarz *et al*. (2013). Chinchilloids represent the first caviomorph lineage to develop hypsodonty, at least during the early Oligocene (Bertrand *et al*., 2012), being likely the first adapted to more arid environments and/or more abrasive diets, conditions already exploited in South America by other mammals such as several lineages of notoungulates (Reguero *et al*., 2010).

Cavioids are comparatively scarce during the Oligocene. In Patagonia they are represented by three species of Cavioidea *s.s*. (Patterson and Wood, 1982), a subgroup within Cavioidea formed by the paraphyletic eocardiids (stem-group) and the family Caviidae (crown-group; Pérez, 2010b). One of them is the mesodont *Asteromys puctus* Ameghino, 1897, the most basal species within Cavioidea *s.s*. (see Pérez and Vucetich, 2012a). The other two species belong to *Chubutomys* [*C. simpsoni* Wood and Patterson, 1959 (Fig. 3.8) and *C. navaensis* Pérez, Krause and Vucetich, 2012], one of the most derived protohypsodont genera of this group (Pérez *et al*., 2012).

Outside Patagonia no representatives of Cavioidea *s.s*. were recorded, but a couple of species have been tentatively assigned to the Cavioidea. *Branisamys luribayensis* Hoffstetter and Lavocat, 1970 from Salla and *Andemys termasi* Bertand *et al*., 2012 from Tinguiririca, have been alternatively assigned to Dasyproctidae and to Dinomyidae (see Bertrand *et al*., 2012 for detailed discussion). Both are relatively large compared to the other taxa, with a slight degree of hypsodonty and tetralophodont cheek teeth. The understanding of their relationships with other caviomorphs depends on thorough phylogenetic analyses and the finding of more and better material.

The peculiar *Cephalomys* Ameghino, 1897 (Fig. 3.9-10) is represented in Patagonia by at least three species (see Vucetich *et al*., 2014c). They have meso- to protohypsodont cheek teeth with an asymmetrical morphology (between lower and upper teeth) that, although not exclusive (the octodontoids *Abrocoma* and *Massoiamys* are examples of this type of morphology), it has been difficult to homologize with that one of other caviomorphs. *Cephalomys* has been diversely considered as a dasyproctid (Wood and Patterson, 1959), a chinchilloid (Landry, 1957; Kramarz, 2001b), or a cavioid *inc. sedis* (Kramarz, 2005), but its relationships need to be analyzed with a broader phylogenetic approach.

Erethizontoids are little diversified, represented by a single genus in Patagonia, *Protosteiromys* Wood and Patterson (1959), and at least another one (unpublished) in Bolivia (Candela, 2000). This is probably the most conservative clade of caviomorphs, as all of them have brachyodont

(to slightly more hypsodont) and bunolophodont or lophodont dental morphologies (the living *Chaetomys* being the single exception; Patterson and Wood, 1982: 394; but see Carvalho, 2000; Martin, 1994b), and are also very similar in skull morphology.

The Deseadan rodents attest to a second caviomorph radiation that represents the first caviomorph diversification in Patagonia (Pérez and Pol, 2012; Vucetich *et al*., 2014c; Arnal and Vucetich, in press). Among Deseadan rodents there are several lineages that independently acquired some degree of hypsodonty. For example in Cabeza Blanca, the richest and most diverse Oligocene fauna (Vucetich *et al*., 2014c), there is a marked trend to develop hypsodonty among different taxa. There are meso- (*Asteromys, Incamys*), proto- (*Chubutomys, Cephalomys*), and euhypsodont (*Scotamys*) taxa with a large variety of simplified occlusal morphologies. They suggest a relatively rapid adaptation to somewhat more open environments/dryer climates, which would have begun to develop more markedly after the cooling of the Eocene-Oligocene boundary (Goin *et al*., 2012). However, the existence in Patagonia of large amounts of volcanic glass in the sediments is likely to have been another trigger for hypsodonty (Strömberg *et al*., 2013).

The early Miocene

Miocene mammal-bearing sediments are widely represented in South America (Figs. 1, 2), and caviomorphs are profusely recorded there.

During the earliest Miocene (Colhuehuapian and "Pinturan" SALMAs; Fig. 2), there is a remarkable diversity of caviomorphs in central Patagonia. More than 36 brachyodont to euhypsodont species have been recognized in the two richest Colhuehuapian faunas, Gran Barranca and Bryn Gwyn (Figs. 1.1.l, n, 2), representing the four superfamilies and more than eight families (Vucetich *et al*., 2010b).

About half of these Colhuehuapian caviomorphs have been considered octodontoids (Vucetich *et al*., 2010b) representing several different lineages. Some of them have no descendants, and have dubious phylogenetic relationships within the superfamily, being recognized as basal octodontoids (Arnal, 2012; Arnal *et al*., 2014) or stem and early divergent crown octodontoids (Arnal and Vucetich, in press; App. 1). Many of these stem octodontoids are restricted to the Colhuehuapian or are older taxa that persisted up to this SALMA. *Protadelphomys latus* Ameghino 1902 and its close relative *Willidewu esteparius* Vucetich and Verzi, 1991, are putative stem octodontoids of uncertain relationships (but see Verzi *et al*., 2014) probably with digging habits, and a dental morphology similar to that of the phiomorph *Gaudeamus* Wood, 1968 (Fig. 3.11). Indeed, dental morphological similarities between *Gaudeamus* and the Peruvian *Sallamys* and *Incamys* led to the inference of caviomorphs in Africa or, alternatively, highlight a remarkable phenomenon of convergence, the latter being a more plausible interpretation (Sallam *et al*., 2011). *Protadelphomys* was originally considered to be an echimyid (Ameghino, 1902) and was tentatively related to *Sallamys pascuali* (Vucetich and Verzi, 1991). It was also related to the living *Carterodon* because they share some dental characters such as upper incisor with a crest on the anterior face, an uncommon feature among Caviomorpha. *Caviocricetus lucasi* Vucetich and Verzi, 1996 is a small species common in central Patagonia with the most terraced molars (Fig. 3.12) known among caviomorphs. This kind of molars suggests a particular

diet within caviomorphs including insects, berries, seeds and small invertebrates (Vucetich and Verzi, 1996: 301); living caviomorphs are essentially herbivorous, and only a few echimyids include non-plant items in their diet (Emmons, 1990). Another group of stem octodontoids are the acaremyids *Galileomys* and *Acaremys,* and *Protacaremys* Ameghino, 1902 (see Verzi *et al*., 2014) originally decribed as an echimyid.

The lineage leading to crown octodontoids is represented by *Paradelphomys* Patterson and Pascual, 1968, described originally as an adelphomyine, but here considered as a putative myocastorine.

Chinchilloids have a relatively poor presence in the Colhuehuapian. They are represented by euhypsodont Neoepiblemidae and Chinchillidae. The latter are represented only by *Eoviscacia australis* Vucetich, 1989*,* whose occlusal pattern is as simplified as those of living viscachas. The euhypsodont neoepiblemids are more abundant and a little more diverse, with several species of *Perimys* Ameghino, 1887a (see Kramarz, 2002).

Cavioids are scarce in the Colhuehuapian (Fig. 2), represented by only two genera, the protohypsodont *Luantus* Ameghino, 1901 with a couple of species (*L. initialis* Ameghino, 1902 and *L. minor* Pérez, Vucetich and Kramarz, 2010), "*Chubutomys* " *leucoreios* Pérez, Vucetich and Kramarz, 2010, and *Australoprocta fleaglei* Kramarz, 1998, which was originally referred to the Dasyproctidae. During the rest of the early Miocene ("Pinturan" and Santacrucian) the record increases greatly with two species of *Neoreomys* Ameghino, 1887a (*N. pinturensis* and *N. australis*) and at least nine species of Cavioidea *s.s*. of the genera *Luantus*, *Phanomys* Ameghino, 1887a, *Schistomys* Ameghino, 1887a, and *Eocardia* Ameghino, 1887a.

Cephalomyids are represented by *Soriamys* Kramarz, 2001b, *Banderomys* Kramarz, 2005, and *Cephalomyopsis* Vucetich, 1985 (Fig. 3.13-14). The latter is an enigmatic taxon, whose dental morphology is somewhat similar to that of the African gundis *Ctenodactylus* (Vucetich, 1989, Vucetich *et al*., 2014d; Vianey-Liaud *et al*., 2010).

This time period is the moment of greatest diversity of erethizontoids (Candela, 2000; Kramarz, 2001a; 2004; 2006a; Kramarz and Bellosi, 2005; Vucetich *et al*., 2010b). Four genera, *Eosteiromys* Ameghino, 1902 (Fig. 4.1), *Parasteiromys* Ameghino, 1904, *Hypsosteiromys* Patterson, 1958, and *Branisamyopsis* Candela, 2003, with several species (see Vucetich *et al*., 2010b) have been recorded. During the Colhuehuapian one of these genera, *Hypsosteiromys* represents the single erethizontid with a hint of hypsodonty (Candela and Vucetich, 2002). This interval also represents the acme of primates in Patagonia (Fleagle *et al*., 1997; Kay, 2010). This coincidence in the fossil record, repeated in other moments (see below), probably is produced by the existence of local environments with forests developed under temperate and humid conditions (Barreda and Palazzesi, 2014).

This great diversity (shown mostly by palatal and jaw fragments), accompanied by an increase in the degree of morphological disparity indicates that caviomorphs occupied a large variety of environments, although most of their modes of life and diet are still difficult to specify (see Álvarez and Arnal, in press, for an example for octodontoids).

Interestingly, several taxa of erethizontids and octodontoids retain generalized characters such as the presence of the deciduous premolar 3 (DP3) in juveniles of *Protadelphomys* (Vucetich *et al*., 2010b; Fig. 3.11) and *Parasteiromys* (see Candela, 1999). *Protadelphomys* in particular, has a mosaic of generalized and specialized characters. Among the generalized ones is the normal

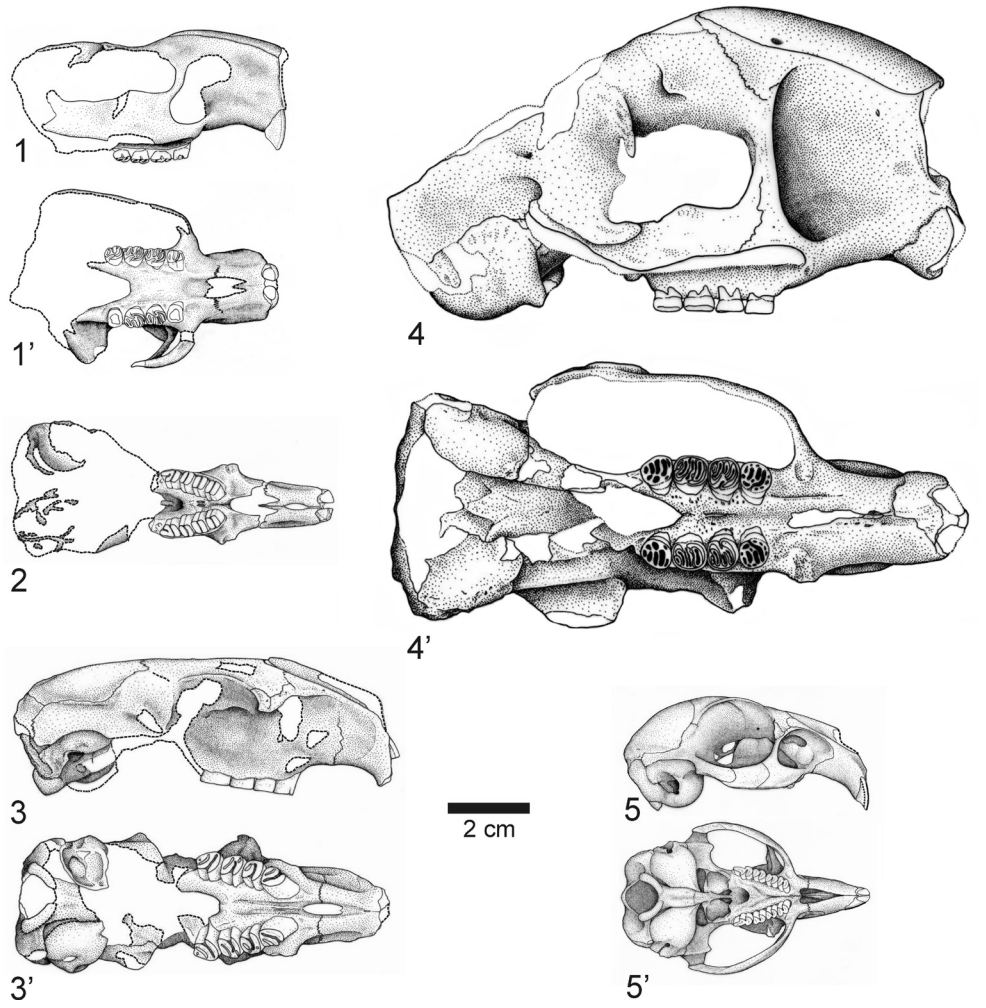


Figure 4. Skulls of erethizontids (1, 4), chinchillids (2), and cavioids (3, 5). 1-1'. *Eosteiromys homogenidens*; 2. *Prolagostomus* sp.; 3-3'. *Alloiomys friasensis*; 4-4'. *Neosteiromys pattoni*; 5-5'. *Dolicavia minuscula*.

replacement of the deciduous premolar 4 (DP4), in addition to the retention of a DP3 in juveniles. A derived character is the high obliquity of the lophs. The "transitional" type of incisor enamel (Vucetich and Vieytes, 2006; Box 1) is a derived character in the context of caviomorphs and a primitive one in the context of Pan-Octodontoidea (Fig. 5).

The rest of the mammal-bearing early Miocene corresponds to the Santacrucian SALMA (Fig. 2). The Santacrucian faunas were first studied by Ameghino (1887a) and played a central role in the understanding of the Miocene Patagonian faunas due to the abundant and excellently-preserved materials collected by Carlos Ameghino (see Scott, 1905; Vizcaíno *et al.*, 2012b). The Santacrucian faunas show a significant change with respect to those Colhuehuapian

and "Pinturan" ones. Octodontoids underwent a reduction in diversity (Vucetich *et al.*, 1999; Arnal, 2012). By contrast, several lineages experienced a progressive increase of hypsodonty, as in acaremyids and myocastorines among octodontoids (Kramarz, 2001a, 2004; Pérez and Vucetich, 2012b; Arnal and Pérez, 2013). The stem group of Cavioidea *s.s.* in particular, achieved euhypsodonty with a simplification of their occlusal pattern (Pérez and Pol, 2012). In addition, these forms greatly increased their specific richness, and *Neoreomys* became common. The taxonomic diversity of erethizontids decreased dramatically; it is represented by only the genus *Steiromys* Ameghino, 1887a. Concomitantly, the monkeys also decreased their diversity; they are represented by only two taxa (Ameghino, 1891; Tejedor *et al.*, 2006).

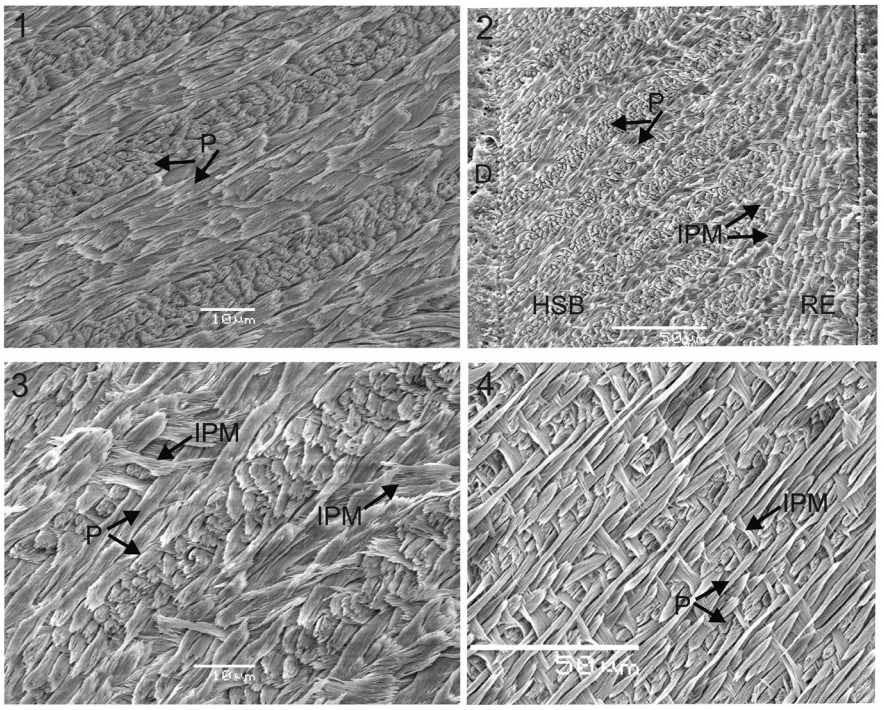
Such gradual increase in hypsodonty followed climatic deterioration with subsequent expansion of open environments, especially manifested in southernmost Patagonia during the Santacrucian. Very slowly, the most brachyodont forms diminished; however, some brachyodont

BOX 1

Incisor enamel evolution

Rodent incisor enamel microstructure is considered a useful tool for rodent phylogeny and systematics (Korvenkontio, 1934; Boyde, 1978; Martin, 1992, 1997). The incisor enamel has generally two layers, one inner portion (PI) with Hunter-Schreger Bands (HSB) and an external portion (PE) formed by radial enamel (RE) (Boyde, 1978; Koenigswald and Clemens, 1992). Among rodents, three types of HSB have been recognized: pauciserial (the most primitive), uniserial, and multiserial (Korvenkontio, 1934; Whalert, 1968; Martin, 1992, 1993, 1997). Multiserial HSB characterizes the Hystricognathi, some Eocene and post-Eocene Ctenodactyloidea, and *Pedetes*. Among Phiomorpha (African hystricognaths) this type is recorded since the late Eocene (Martin, 1992, 1993, 1994a). Classically three multiserial HSB subtypes have been recognized in which the interprismatic matrix (IPM) may run parallel (the most primitive subtype), at an acute angle (approximately 45°), or at right angles (rectangular) with respect to the prisms, this last considered to be the most derived (Martin, 1992, 1993, 1994a). Among caviomorphs, the first two subtypes are present in the superfamilies Chinchilloidea, Cavioidea, and Erethizontoidea, whereas the most derived subtype is restricted to the Octodontoidea and considered a synapomorphy of this superfamily (Martin, 1992). These three subtypes are already present in what are currently considered the most ancient caviomorphs (pre-Deseadan? of Santa Rosa, and Deseadan; Martin, 1992, 2004, 2005), but the incisor enamel of the Contamana and Tinguiririca rodents has not been studied yet. However, a transitional stage between the acute and rectangular subtypes was described for several Deseadan to "Colloncuran" (late Oligocene-middle Miocene) octodontoids (=Pan-Octodontoidea) (*e.g.*, *Sallamys*, *Caviocricetus*, *Protadelphomys*, *Willidewu*, *Plesiacarechimys* and two taxa indet. of La Cantera; Martin, 1994b:126; Vieytes, 2003; Vucetich and Vieytes, 2006). The discovery of this transitional subtype of HSB, recorded as homoplasy in different taxa, allows new interpretations about the early evolution of octodontoids (Vucetich and Vieytes, 2006; Vucetich *et al.*, 2010a; Arnal *et al.*, 2014).

The presence of transitional IPM in different Pan-Octodontoid lineages, together with rectangular IPM in lineages not closely related to each other (*e.g.*, Acaremyidae and Octodontidae; Vucetich and Kramarz, 2003) suggests independent development of the most derived subtype of HSB (Saether, 1979; Koenigswald, 1997) in different lineages of this monophyletic group, after the caviomorphs arrived in South America (Vucetich and Vieytes, 2006; Vucetich *et al.*, 2010c). On the other hand, it could have evolved once, thus becoming a synapomorphy for the Pan-Octodontoidea; if this were so, *Caviocricetus*, *Sallamys-Protadelphomys-Willidewu*, and *Plesiacarechimys* would represent different lineages within stem Octodontoidea (but see Arnal *et al.*, 2014). Any of these interpretations would reinforce the hypothesis that the early evolution of the octodontoids was more complex than previously supposed (Reig, 1989: 262; Vucetich and Kramarz, 2003; Arnal *et al.*, 2014).



Microphotographs of the incisor enamel of two incisors in longitudinal section. 1, 2 and 3. Caviomorpha indet. from La Cantera, 1. detail of the Hunter-Schreger Bands (**HSB**) with parallel to acute interprismatic matrix (**IPM**); 2. detail of the HSB with acute IMP; 3. detail of the HSB with transitional IPM; 4. *Ctenomys* sp., detail of the HSB with rectangular IPM. **D**, dentine; **P**, prism.

species persisted until at least the early middle Miocene in northern Patagonia (Vucetich, 1994; Vucetich *et al.*, 1993a; Vucetich and Vieytes, 2006) together with the last Patagonian monkeys (Kay *et al.*, 1998).

The middle Miocene

Although poorly known, the middle Miocene ("Colloncuran", Laventan, and "Mayoan" SALMAs, plus "El Petiso", Fig. 2) is one of the most interesting periods for caviomorph evolution, especially from the point of view of the origin of modern taxa. Both paleontological (Vucetich *et al.*, 1999; Pérez, 2010a, b; Vucetich and Pérez, 2011; Pérez and Pol, 2012) and neontological (Dunnum and Salazar-Bravo, 2010a, b; Opazo, 2005; Poux *et al.*, 2006; Pérez and Pol, 2012; Upham and Patterson, 2012; Upham and Patterson, this volume) evidence states that the lineages that led to the differentiation of most of the living taxa likely originated during this time (but see Verzi *et al.*, 2014).

The octodontoids from the middle Miocene are represented in Patagonia by several poorly-known species, *e.g.*, *Galileomys* sp. Vucetich and Kramarz, 2003, *Protacaremys denisae* Vucetich *et al.*, 1993a, *Maruchito trilofodonte* Vucetich *et al.*, 1993a, *Plesiacarechimys koenigswaldi* Vucetich and Vieytes, 2006, and *Sciamys petisensis* Arnal and Pérez, 2013 (the youngest and most hypsodont acaremyid), and several unnamed taxa found in the Cerro Boleadoras Formation (Vucetich, 1994, see App. 1). *Plesiacarechimys koenigswaldi* is especially interesting in this context because it shows the survival in northern Patagonia of an old lineage that retains primitive characters such as the transitional incisor enamel (Box 1) and generalized dental morphology. This species has also been recorded in the late Miocene of Entre Ríos (Candela *et al.*, 2012a) suggesting a biogeographic connection between the northeast of Argentina (Paraná River) and northern Patagonia (Fig. 1.1.k, 1.2.l).

Chinchilloids are represented by several species of the chinchillids *Prolagostomus* (Fig. 4.2) and *Pliolagostomus* that became more frequent than in the Santacrucian. The neoepiblemid *Perimys*, so frequent in the Santacrucian, is not recorded in the "Colloncuran" but is represented in the Cerro Boleadoras Formation (Vucetich, 1994).

A few species of Cavioidea from the middle Miocene were assigned to Dasyproctidae, such as *Neoreomys australis* Ameghino, 1887a, *Alloiomys pattersoni* Vucetich, 1979 (Fig. 4.3), and the Bolivian *Mesoprocta hypsodus* Croft *et al.*, 2011. However, their assignment to this family is dubious (Vucetich, 1984), and at least *Neoreomys* could be more closely related to the "eocardiids" than to living dasyproctids (Pérez, 2010a, b). A better understanding of the relationships of these taxa requires additional phylogenetic analyses with a larger taxon and character sampling. Besides, by these times ("Colloncuran" –post Colloncuran) six species of the stem group of Cavioidea *s.s.* are recorded (*Eocardia robertoi* Vucetich, 1984, *E. robusta* Vucetich, 1984, *Matiamys elegans* Vucetich, 1984, *Microcardiodon huemulesis* (Kraglievich, 1930), *M. williensis* Pérez and Vucetich, 2011 and *Guiomys unica* Pérez, 2010b). One of the most interesting species is *G. unica*, found in El Petiso (Chubut, Argentina; Villafañe *et al.*, 2008) and Quebrada Honda (Bolivia; Croft *et al.*, 2011). It is interesting because it has mandibular and dental characters intermediate between the basal Cavioidea *s.s.* and the family Caviidae (Pérez, 2010). Later, the "Mayoan" record of Cavioidea is extremely scarce ("Mayoan gap", Pérez and Pol, 2012; Figs. 2, 7) with only one isolated molar of Cavioidea *s.s.* (*Cardiomys? andinus*) which was considered by Vucetich and Pérez (2011) to be the oldest hydrochoerine.

Although represented by scant materials, porcupines were more diverse at this time than in the Santacrucian. They have been recorded in a single locality, Cañadón del Tordillo in Neuquén (Vucetich *et al.*, 1993a; Fig. 1.1.k), by three species representing three different lineages: *Branisamyopsis*, *Steiromys*, and *Neosteiromys*? (Candela, 2003; Candela and Morrone, 2003). In this case the monkeys apparently did not follow the diversity of porcupines, as they are here represented by only a single species (Kay *et al.*, 1998).

Early–middle Miocene mammal faunas, similar in family and genus composition to the Argentinean ones have been found in several localities in Chile (Flynn *et al.*, 2002; 2008; Bostelmann *et al.*, 2013); this is the classical middle Miocene fauna of the Río Cisnes (Fig. 1.1.r) that provided the basis for the recognition of the "Friasian" Age (Kraglievich, 1930; Vucetich, 1994; Marshall and Salinas, 1990).

The late Miocene

The late Miocene (Chasicoan and Huayquerian SALMAs, Fig. 1.2) is well represented in central and northern Argentina, with three most important areas: Northwest (Fig. 1.2.i, q), Northeast (Fig. 1.2.l), and Pampean region (Fig. 1.2.r, s). Northeast and Northwest areas represent clearly different biogeographic areas, the former being dominated by a diversity of environments related to the pre-Paraná River, under warm and humid conditions and with the development of gallery forests (see Brandoni and Noriega, 2013). Many modern caviomorph lineages have their first record, or became abundant during this period.

During these times crown-octodontoids became very rich and diverse, especially in the Huayquerian (Figs. 1.2, 2), represented by taxa clearly related to modern lineages. For example, among the echimyids *Theridomysops* Vucetich, 1995 is closely related to the living *Clyomys* and *Euryzygomatomys*; *Pampamys* Verzi *et al*., 1995, is related to *Thrichomys*, whereas *Reigechimys* Verzi *et al*., 1994, is related to extinct Brazilian forms that lived up to the Quaternary, such as *Dicolpomys* Winge, 1888 (Hadler *et al*., 2008). Likewise, the first abrocomids are known from the Huayquerian (but see Verzi *et al*., 2014) with *Abrocoma antiqua* Rovereto, 1914 and *Protabrocoma paranensis* Kraglievich, 1927.

In addition, several small brachyodont to mesodont caviomorphs recorded in Mendoza (Fig. 1.2.q) and Catamarca (Fig. 1.2.i), were erroneously referred to the most typical Pliocene genus *Eumysops* (see Rovereto, 1914; Vucetich, 1995; Olivares *et al*., 2012).

An interesting issue is the acquisition of high degrees of hypsodonty, up to euhypsodonty among Octodontidae (Verzi, 2002). Several lineages, well recorded in different levels and localities of the Cerro Azul Formation (La Pampa; Fig. 1.2.r), provide one of the best examples of this process. In the lineages of *Chasichimys-Xenodontomys* (Ctenomyinae; Verzi *et al*., 2004), *Neophanomys* (Octodontinae; Verzi *et al*., 2011), and *Reigechimys* (Echimyidae; Verzi *et al*., 1994; Sostillo *et al.,* 2014) a progressively increasing hypsodonty occurred together with changes of the dental gross morphology (*e.g*., variation in the persistence of flexi/ids toward a simplification of the occlusal surface) and a modification of the enamel microstructure of the cheek teeth. This latter consists of the gradual secondary acquisition of radial enamel (RE) in the enamel pattern, first recorded in caviomorph rodents of the *Chasichimys-Xenodontomys* lineage (Verzi *et al*., 2004). Such acquisition of RE strengthens the single enamel layer remaining as leading edge in the ctenomyine cheek teeth. These changes would represent a response to a more abrasive diet in progressively more desertic environments (Verzi *et al*., 2004) that occurred as a result of the global cooling and drying trend (Pascual and Ortiz Jaureguizar, 1990; Janis, 1993; MacFadden and Cerling, 1996). This suggests that in caviomorphs the enamel pattern evolved in response to different functional requirements (Vieytes, 2003; Álvarez *et al*., this volume).

Chinchilloids have their acme at the Huayquerian (Fig. 2). They are represented by the lagostomine *Lagostomus* (*Lagostomopsis*) Kraglievich, 1926, the gigantic neoepiblemids *Phoberomys* and *Neoepiblema*, probably of semiaquatic habits, and a great diversity of terrestrial eumegamyines (Dinomyidae). Excluding the octodontoids, dinomyids are one of the most diverse groups of caviomorphs with nearly 20 genera (App. 1), medium to large-sized, with multilaminated proto- to euhypsodont teeth, a great diversity of cranio-mandibular morphologies, and a wide distribution in central and northern Argentina, Brazil, and Uruguay (Frailey, 1986; Francis and Mones, 1966; Nasif, 2009; Nasif *et al*., 2013; Perea *et al*., 2013; Rinderknecht *et al*., 2011a). This suggests that fossil dinomyids (the eumegamyines *in. lit.*) had diverse life strategies in varied environments.

Cavioids were very diverse in this period. Among them, the lineage of the caviid hydrochoerines reached their greatest diversity, especially during the Huayquerian, through a variety of the large semiaquatic capybaras, and the terrestrial extinct "cardiomyines" (Vucetich *et al*., 2011, 2012; Deschamps *et al*., 2013). Capybaras are represented by several species of *Cardiatherium* (Vucetich *et al*., 2005a, 2014a; Deschamps *et al*., 2007, 2013) that apparently had already achieved some biological and behavioral characteristics of modern capybaras, such as semiaquatic habits and living in herds. The extinct "cardiomyines" were diverse and abundant, and are represented by several genera and species (*Xenocardia* Pascual and Bondesio, 1963*, Procardiomys* Pascual, 1961, *Cardiomys* Ameghino, 1885, and *Caviodon* Ameghino, 1885; App. 1). They had a wide geographic distribution and, unlike hydrocherines, probably terrestrial habits. For example, in the Andalhuala Formation "cardiomyines" are recorded in the basal water-related levels together with capybaras (*Paraeuphractus prominens-Cardiomys ameghinorum-Cardiatherium* Zone) and continue up to the upper levels –despite the aridification trend (*Vassallia maxima-Pseudoplataeomys-Pithanotomys* Zone)– where capybaras are absent (see Esteban *et al*., 2014). Caviines and dolichotines are also abundantly recorded in this period: *Allocavia* Pascual, 1962, *Neocavia* Kraglievich, 1932, *Prodolichotis* Kraglievich, 1932, *Pliodolichotis* Kraglievich, 1927, and *Paleocavia* Ameghino, 1889. These genera have several nominal species, which have not been revised recently. *Paleocavia* is a very interesting taxon because it shows similar dental characters to the living *Cavia* (Verzi and Quintana, 2005).

Erethizontoids were still diverse at this time. They are represented by the large *Neosteiromys bombifroms* Rovereto, 1914 and *N. pattoni* Candela, 2004 (Fig. 4.4) from the Andalhuala Formation, Catamarca (Fig. 1.2.i), *Paradoxomys cancrivorus* Ameghino, 1885 from the "conglomerado osífero" (see below), and another one, probably a third genus, from San Luis province (Pascual and Bondesio, 1981; Candela, 2004). The strong masticatory apparatus of *Neosteiromys* suggests they were adapted to more abrasive food and inhabited more open environments than the living porcupines (Candela, 2004).

A well-known fauna for its role in the history of the knowledge of Miocene mammals, is that from the "conglomerado osífero" of the Ituzaingó Formation, exposed at the cliffs of the Paraná River (Fig. 1.2.l), also known as "Mesopotamiense" (see Cione *et al*., 2000). A great number of rodents with an important taxonomic diversity and morphological disparity is recognized in these sediments (Cione *et al*., 2000; Candela *et al*., 2012a; Nassif *et al*., 2013). The octodontoids from these sediments, unlike those of La Pampa, are represented almost exclusively by "echimyids": "*Eumysops*" *parodii* and *Haplostropha scalabriniana*; the myocastorines *Myocastor paranensis* and *M. obesus* have been also mentioned in descriptions of this fauna. The presence of the abrocomid *Protabrocoma paranensis* with a dental morphology very similar to that of the living species of the Andean *Abrocoma* is noteworthy. Chinchilloids are the most outstanding group. They are represented by one species of *Lagostomus* Brookes, 1928, the gigantic neoepiblemids *Phoberomys* and *Neoepiblema*, and an overwhelming diversity of dinomyids, the greatest known for one locality with more than 30 species. These dinomyids ranged from protohypsodont and medium-sized species (*Paranamys typicus*, *Potamarchus murinus*, and *P. sigmodon*) to euhypsodont, large-sized species (*Gyriabrus holmbergi* and *G. rebagliatti*, several species of "*Tetrastylus*", *Carlesia pendolai*, *Eumegamys paranensis* (Fig. 10.5), *Isostylomys laurillardi*, *Eumegamysops praependens*; (Fig. 10.8) see App. 1 and Nasif *et al*., 2013). Cavioids are represented by one species of capy-

bara, *Cardiatherium paranense* (Ameghino, 1883) and several species of "cardiomyines" *Cardiomys* and *Caviodon* (Vucetich *et al.*, 2005a, 2011), as well as *Paleocavia*, *Pliodolichotis* and *Prodolichotis* (Cione *et al.*, 2000; Nasif *et al.*, 2013). Erethizontids are represented by the large *Paradoxomys cancrivorus*, not related to the coeval *Neosteiromys* from Catamarca but closely-related to the living *Coendou*, being the oldest representative of the living porcupines (Vucetich and Candela, 2001; Candela and Morrone, 2003). Although many of these taxa have a wide geographic distribution (*e.g.*, *Cardiatherium*) some of them belong to typical Patagonian lineages (*e.g.*, *Protabrocoma* and *Lagostomus*), and others seem to be the southern expansion of Brazilian lineages (*e.g.*, *Phoberomys* and *Paradoxomys*). Thus, this region appears to be a transition zone (Morrone, 2006: 469).

The Pliocene

During the Pliocene the caviomorphs of central Argentina experienced a strong impoverishment due to the reduction in diversity of Dinomyidae and Echimyidae, the local extinction of Erethizontidae, and the extinction of Neoepiblemidae. This change was probably driven by climatic changes and the impact produced by the mammals of Holarctic origin participating in the Great American Biotic Interchange (GABI; Webb, 1985; Morgan, 2008; Woodburne, 2010).

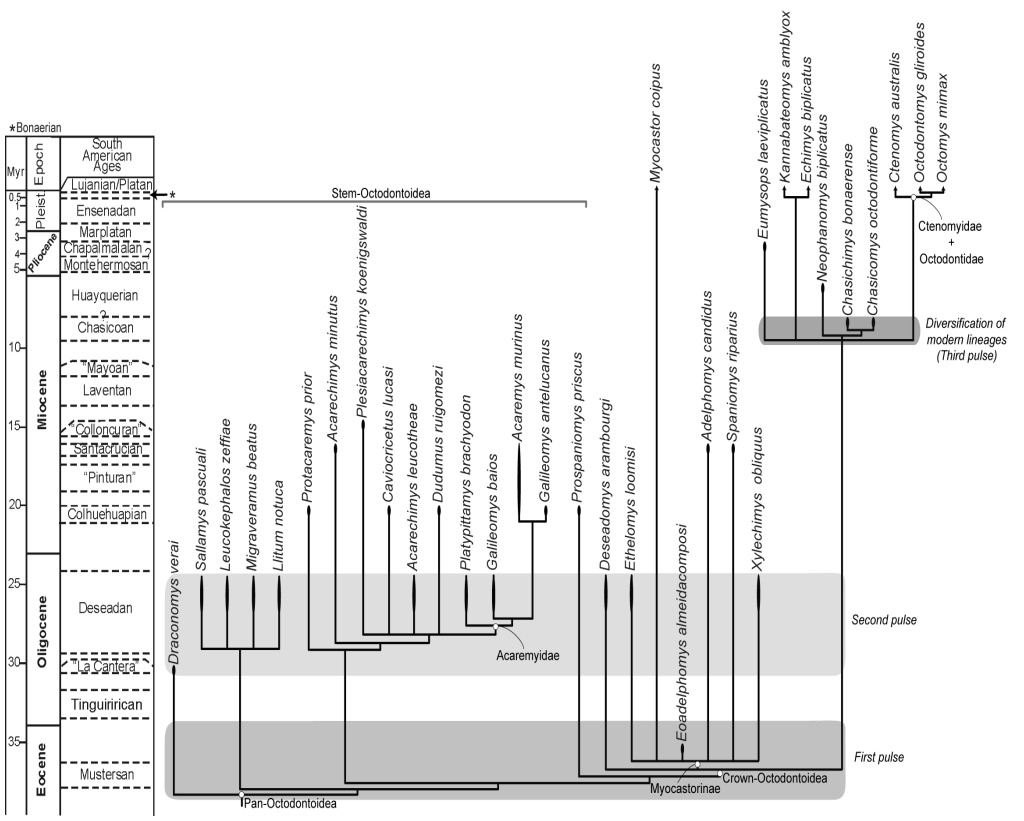


Figure 5. Evolutionary hypothesis of Octodontoidea based on phylogenetic analyses of Arnal and Vucetich (in press). Gray areas show main radiation events.

However, among octodontoids there is a notable diversification of Octodontidae probably associated also with climatic changes. The octodontids are common in the Pliocene of central and northwestern Argentina with the genera *Neophanomys*, *Phtoramys*, *Pithanotomys*, and *Pseudoplataeomys* (Marshall and Patterson, 1981; Deschamps *et al*., 2012; Tomassini *et al*., 2013). Ctenomyids, as well, are abundantly recorded with the genera *Eucelophorus* (the most specialized tooth-digger; Verzi and Olivares, 2006; Vieytes *et al*., 2007), *Actenomys*, *Praectenomys*, *Paractenomys*, and *Ctenomys*, which acquired different adaptations to digging and life underground (Verzi and Olivares, 2006; Lessa *et al*., 2008). *Eucelophorus* and *Ctenomys* independently acquired subterranean habits, whereas *Actenomys* probably had fossorial habits, spending part of its life above the surface (Verzi, 2008). "Echimyids" are represented by only *Eumysops* Ameghino, 1888 (Olivares *et al*., 2012; Olivares and Verzi, 2014) while *Paramyocastor,* usually considered an extinct "echimyid" (Verzi *et al*., 2002), represents a crown-octodontoid related to *Myocastor* (see Fig. 5). *Paramyocastor* is the only non-euhypsodont Pliocene caviomorph of southern South America. By the end of the Pliocene, a strong climatic deterioration can be recognized in Buenos Aires Province (Chapadmalal area; Fig. 1.2.t) through the record of the desert-adapted octodontoids *Abalosia* (a genus related to the living *Tympanoctomys*), *Pithanotomys*, and *Abrocoma* (Verzi and Quintana, 2005).

Chinchilloids are represented by several species of the chinchillid *Lagostomus*, with the diversity of chinchillines being conspicuously greater than today (Ameghino 1888, 1908). Nevertheless, the validity of these taxa must await a systematic revision (Francis and Mones, 1965; Rasia and Candela, 2013). Dinomyids were very scarce but still a few gigantic representatives inhabited central Argentina and Uruguay (see below).

Cavioids were abundant and diverse but are still poorly studied. Caviines are represented by the extinct genera *Neocavia* (Kraglievich, 1932)*, Dolicavia* (Ameghino, 1906; Fig. 4.5)*,* and *Paleocavia*, and the living *Cavia, Galea* (=*Pascualia* Ortega Hinojosa, 1963), and *Microcavia*, which are first recorded during this time (see Quintana, 1996, 1998; Verzi and Quintana, 2005). Dolichotines are represented by *Dolichotis chapalmalense* (=*Orthomyctera chapalmalense* Ameghino, 1889). Many species of *Prodolichotis* and *Orthomyctera* are recorded, being alternatively included in Dolichotinae or Caviinae, but these genera are a taxonomic hodge-podge and their numerous nominal species need a detailed revision.

Hydrochoerines are represented by *Hydrochoeropsis dasseni* Kraglievich, 1930, and at least three species of *Phugatherium* Ameghino, 1887b (Vucetich *et al*., 2014a; Figs. 9.1-2), which include the largest capybaras so far known (see below). Only *Caviodon* is still recorded among "cardiomyines", with several species in central Argentina: *C. australis* (Ameghino, 1888), *C. pozzi* Kraglievich, 1927, and *C. cuyano* Vucetich *et al*., 2011 (Fig. 10.1).

Pleistocene-Holocene

During this interval, the succession of glacial and interglacial periods played an important role in the setup of the mammal assemblages. Specific differences in the reaction to these changes resulted in the association of species that are today allopatric forming nonanalog assemblages typical of the Pleistocene (Bell *et al*., 2004). The legions of mammals that entered through the Panama corridor during the main phase of the GABI certainly contributed to shape the Quaternary faunas. In the case of caviomorphs, the modern taxonomic composition was

already established (Vucetich and Verzi, 1999). Only fluctuations in their geographic distribution are seen as a response to climatic oscillations (glacial-interglacial). This is best recorded in an ecotonal area such as the Buenos Aires Province. Brazilian elements (such as the echimyid cf. *Clyomys* and the dasyproctid *Plesiaguti totoi* Vucetich *et al*., 1997; Vucetich and Verzi, 2002; Vucetich *et al*., 2005b) along the Atlantic coast attest to warm pulses. Opposite climatic conditions are evidenced by the caviid *Dolichotis salinicola* (Burmeister, 1875) and the octodontine desert-adapted *Tympanoctomys cordubensis* (Ameghino, 1889) recorded in the Pleistocene of the coastal area (Tonni, 1981; Verzi *et al*., 2002 respectively). Outside of Buenos Aires Province, a nice example of a nonanalog assemblage was found in the Sopas Formation of northern Uruguay (Fig. 1.2.k) where the porcupine *Coendou*, the crown octodontoid *Myocastor*, and the caviids *Galea* and *Microcavia* were recorded together (Ubilla and Perea, 1999).

The great late Pleistocene extinction of large and megamammals (mostly xenarthrans, notoungulates, litopterns, equids, and gomphotheres) did not include the gigantic rodents which had already suffered a major extinction by the end of the Pliocene, of which the hydrochoerine *Neochoerus* –and perhaps the dinomyid *Josephoartigasia*– were the only survivors (see below).

The intertropical record

As noted above, the caviomorph fossil record in intertropical areas (the modern Brazilian Subregion, Fig. 1) is much poorer than that of southern South America. The oldest records belong to Contamana and Santa Rosa (Peru, see above; Fig. 1.1.b, c) in which almost exclusively brachyodont species are found. For the Deseadan only two Brazilian species are known, *Sallamys*? *minutus* Vucetich and Ribeiro, 2003, and *Paulacoutomys paulista* Vucetich *et al*., 1993b, both referred originally to Echimyidae. Based on new cladistic analyses (Arnal and Vucetich, in press both species appeared to be stem-octodontoids rather than echimyids.

By contrast, the Miocene record is much richer and indicative. In the La Venta fauna (Laventan SALMA, middle Miocene, Colombia; Figs. 1.1.a, 2; Fields, 1957; Walton, 1997) there are some brachyodont or slightly higher crowned taxa referred by Walton (1997) to the families Echimyidae (*Acarechimys*, *Ricardomys*) and Erethizontidae (*Steiromys*, *Microsteiromys*); but most of the fauna is composed of high-crowned protohypsodont or euhypsodont forms (Fields, 1957). Among them, there are basal caviids such as *cf. Guiomys* (Pérez, 2010a), and other caviids such as *Prodolichotis pridiana* Fields, 1957 and Dolichotinae indet. (see Walton, 1997). Other taxa have uncertain relationships such as *Neoreomys*, *Microscleromys*, *Olenopsis*, "*Scleromys*" which have been referred to Dasyproctidae and/or Dinomyidae (Fields, 1957; Walton, 1997; Candela and Nasif, 2006; Kramarz, 2006b). More inclusive phylogenetic analyses are needed to resolve their relationships. In this fauna, some taxa with a wide geographic distribution up to Patagonia (*Acarechimys*, *Neoreomys*, *Steiromys*) coexisted with endemic taxa (*Microscleromys* and *Microsteiromys*) and others of intertropical distribution (*Ricardomys;* Madden and Vucetich, unpublished data). However, there were no acaremyids, chinchillids, or neoepiblemids, so frequent in the Miocene faunas of Patagonia. No capybaras have been reported; although their presence would have been expected in a warm intertropical fauna of this age (see Pérez and Pol, 2012). But some of the materials referred by Walton (1997) to *Prodolichotis pridiana* (*e.g.,* Walton, 1997 Fig. 24.7.I) could be "cardiomyines" based on their dental morphology (p4 with three

complete lobes and an internal fissure in each lobe of m1-m3, see Vucetich and Pérez, 2011).

The contemporaneous fauna of Quebrada Honda (Bolivia; Croft *et al.*, 2011; Fig. 1.f.), is very interesting due to its geographical position between La Venta and Patagonia, within a cordilleran environment. Its rodent fauna (Croft *et al.*, 2011) is more similar to those of Patagonia, especially due to the presence of abundant chinchillids. However, as at La Venta, Quebrada Honda has some endemic taxa (*Mesoprocta hypsodus* Croft *et al.*, 2011, *Quebradahondomys potosiensis* Croft *et al.*, 2011) together with others of wide distribution (*Guiomys*, *Acarechimys*).

The late Miocene (Huayquerian SALMA, Fig. 2) of the Acre region in Brazil (Fig. 1.1) as well as in the adjacent area in Peru, has yielded numerous taxa among which there are capybaras, caviids, "cardiomyines", the gigantic neoepiblemids, some dinomyids, several poorly known brachyodont species of echimyids, and probably erethizontids, plus the oldest undoubted Dasyproctidae (Frailey, 1986; Sant'Anna, 1994; Campbell *et al.*, 2006; Antoine *et al.*, 2013; Kerber *et al.*, in press a). Studies in progress (Vucetich and Campbell, in prep.) suggest that as foreseen by some phylogenetic analyses (Fabre *et al.*, 2013), forms related to the living echimyids *Thrichomys* and *Proechimys* would have been present among the microrodents of this interval. In the Huayquerian of Venezuela, *Cardiatherium*, *Eumegamys* (Pascual and Díaz de Gamero, 1969), and the well known gigantic neoepiblemid *Phoberomys pattersoni* Mones, 1980 (see below) are recorded.

The Pliocene record is scanty. In Venezuela it is represented by isolated fragments of hydrochoerines, "cardiomyines", *Phoberomys*, *Neoepiblema* and a probable octodontoid *Marisela gregoriana* Vucetich *et al.*, 2010a found in the San Gregorio Formation of Falcón State (Fig.1.2.a). Recently, a Pliocene capybara was reported from northern Colombia (Moreno-Bernal *et al.*, 2013).

Our knowledge of the Quaternary rodents of Brazil began with the studies of Peter Lund in the first half of the XIX Century, with the discovery of fossils in the caverns of Lagoa Santa (Fig. 1.2.f; for an enjoyable story of these discoveries see Cartelle, 1994). Many other rodent faunas have been described since then, covering a wide region of eastern Brazil (*e.g.*, Hadler *et al.*, 2008; Kerber and Ribeiro, 2012; Kerber *et al.*, 2011, 2014, in press b; Oliveira *et al.*, 2013 and literature therein; Fig. 1.2.c-f, j). These rich faunas include numerous taxa with living representatives (*Coendou*, *Cavia*, *Kerodon, Hydrochoerus, Dasyprocta, Cuniculus*, *Dactylomys, Trinomys*, *Echimys*, *Mesomys*, *Nelomys*, *Callistomys, Carterodon, Myocastor*) showing a great diversity of echimyids. This assemblage proves that the modern caviomorph fauna of eastern Brazil was already established. However, extinct taxa, such as the echimyid *Dicolpomys* and the "eumegamyid" *Tetrastylus* show the survival in lower latitudes of lineages which became extinct earlier in higher latitudes. As well, the record of *Lagostomus* (Kerber *et al.*, 2011) and *Myocastor* (Kerber *et al.*, 2014), north of their modern distribution is especially interesting because it demonstrates the occurrence of cold pulses.

Evolutionary history

The most accepted theories state that rodents arrived in northern South America by rafting from Africa during the early to middle Eocene (Houle, 1998; Rowe *et al.*, 2010; Vucetich *et al.*, 2010c; Antoine *et al.*, 2012).

The fossil record together with phylogenetic analyses based on morphological data, show that

the evolutionary history of caviomorphs occurred through pulses of diversification. The major events occurred in the middle? Eocene-early Oligocene (Vucetich *et al.*, 1999; Arnal and Vucetich, in press), late Oligocene (Pérez and Pol, 2012; Arnal and Vucetich, in press), and middle to late Miocene (Vucetich *et al.*, 1999; Pérez and Pol, 2012; Arnal and Vucetich, in press) (Fig. 5-7).

Although the middle Eocene–early Oligocene caviomorph record is poorly known, this interval was a key moment for the evolutionary history of the group. The relationships of Contamana rodents are still controversial. Some of them have been interpreted as stem caviomorphs not included in any of the modern superfamilies (Antoine *et al.*, 2012; Arnal *et al.*, 2014; Arnal and Vucetich, in press). The fauna of Santa Rosa, taxonomically richer than that of Contamana, otherwise shows that at least three of the four main lineages (Octodontoidea (Erethizontoidea + Cavioidea)) were already differentiated (Antoine *et al.*, 2012; Arnal *et al.*, 2014; Arnal and Vucetich, in press; Fig. 6.1). However, phylogenetic analyses are still in need to prove the relationships of these taxa among caviomorphs. These faunas would represent the first pulse of radiation that occurred in intertropical South America (Fig. 5).

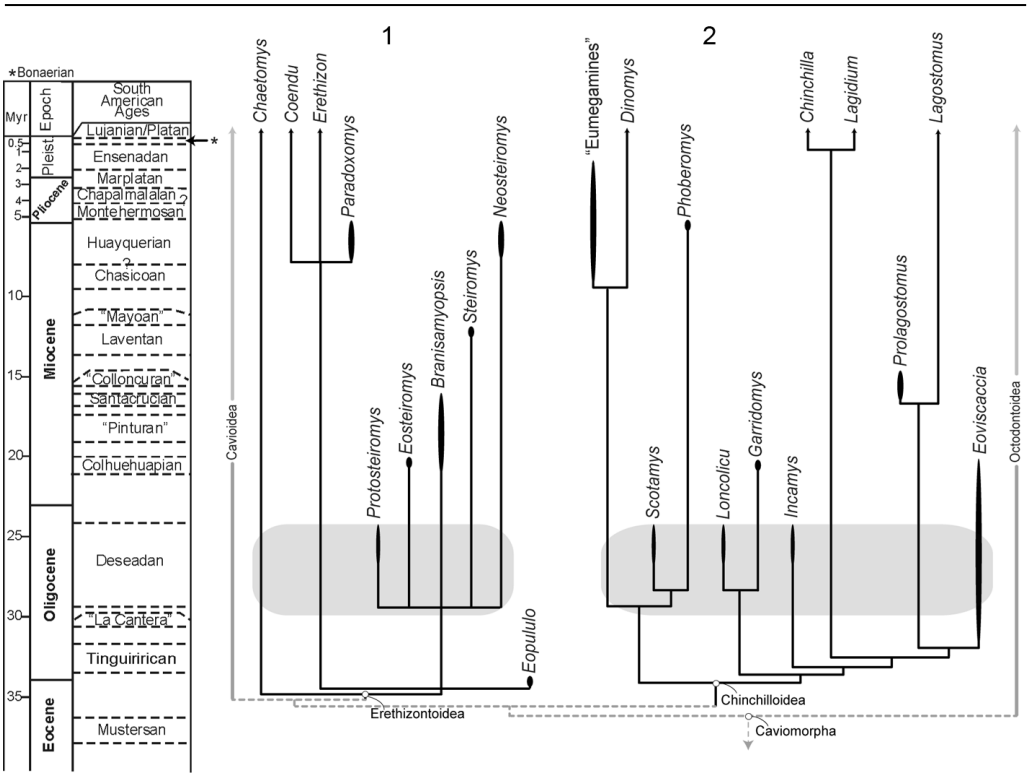


Figure 6. Graphical representation of evolutionary hypothesis of, 1. Erethizontoidea and, 2. Chinchilloidea based on phylogenetic analyses of Candela (2004), Kramarz *et al.* (2013), Sánchez Villagra *et al.* (2003), Antoine *et al.* (2012), Arnal *et al.* (2014), Arnal and Vucetich (in press), as well as on data in Vucetich *et al.* (2014c). Superfamilial relationships based on molecular data (Houchon and Douzery, 2001; Fabre *et al.*, 2012, 2013; Upham and Patterson, this volume) differ from the hypothesis presented here. Gray areas = second pulse of radiation.

Caviomorphs are first recorded in high latitudes in the earliest Oligocene of central Chile (Bertrand *et al.*, 2012 and literature therein) although they could have reached this area somewhat earlier. As a novelty, the fauna of Tinguiririca includes the oldest recognized chinchilloid. In central Patagonia they are first recorded a little later, during the early Oligocene (Vucetich *et al.*, 2010c; Figs. 1.1.h, n, 2). This southern migration likely occurred in response to the Eocene–Oligocene cooling that probably favored the settlement of new environments (Goin *et al.*, 2012; Fig. 2).

A second radiation, that also implies the first radiation detected in Patagonia, probably occurred during the earliest Oligocene and/or during most of the Oligocene (Arnal and Vucetich, in press). This is inferred from the rich record of the Deseadan SALMA (Fig. 2; Wood, 1949; Wood and Patterson, 1959; Hoffstetter and Lavocat, 1970; Patterson and Wood, 1982; Vucetich, 1989; Vucetich and Ribeiro, 2003; Pérez and Pol, 2012; Pérez *et al.*, 2012; Vucetich *et al.*, 2014c, d), showing that a moderate radiation had also occurred at least in three of the four superfamilies: Octodontoidea, Chinchilloidea, and Cavioidea (Figs. 5-7). Phylogenetic analyses of Octodontoidea (Arnal, 2012; Arnal *et al.*, 2014; Arnal and Vucetich, in press) indicate that its early evolutionary history was characterized by the differentiation of successive lineages that survived until the early or middle Miocene with no direct relationships with modern families (Fig. 5). Modern lineages are represented by a few taxa (*e.g.*, *Xylechimys*) although the diversity must have been higher because of the finding of several ghost lineages in phylogenetic analyses (Arnal and Vucetich, in press; Fig. 5).

The early radiation of chinchilloids (Fig. 6.2) also appears to be characterized by the differentiation of some taxa not directly related to modern lineages (Kramarz *et al.*, 2013; Vucetich *et al.*, 2014c); but the presence of *Eoviscaccia frassinetti* suggests that the lineage of living chinchillids was already differentiated in the Tinguiririca (early Oligocene; Bertrand *et al.*, 2012; Kramarz *et al.*, 2013).

Concerning erethizontoids, Candela (2004), based on a morphological phylogenetic analysis, proposed a basal dichotomy giving origin to the clade of the living forms and to that of the Oligocene–Miocene porcupines of Patagonia for which she proposed the subfamily Steiromyinae (Fig. 6.1). As in other groups (*e.g.*, "Echimyidae", platyrrhine primates; Patterson and Pascual, 1968; Kay *et al.*, 2008) it appears that the southern porcupines evolved separatedly from their intertropical representatives.

A recent phylogenetic analysis (Pérez and Pol, 2012) based on morphological and molecular data and calibrated with the geological age of the fossil taxa shows three major radiations in the evolutionary history of Cavioidea *s.s.* (Fig. 7). The first one is the radiation of the stem group of Cavioidea *s.s.* during the late Oligocene in the Deseadan SALMA. This was revealed through the record of three species and the presence of at least six ghost lineages in the phylogenetic analyses (Pérez, 2010b) that would extend back their age at least four million years before their first appearance in the fossil record of the early Miocene. The discovery of this Deseadan radiation contrasts with the traditional hypotheses that propose that the earliest evolutionary history of Cavioidea *s.s.* would have occurred through gradual changes from the Oligocene up to the early Miocene (see Kramarz, 2006a). The analysis of Pérez and Pol (2012) rejects such hypotheses because of the derived phylogenetic position of *Chubutomys*. These authors stated that during this radiation different evolutionary novelties were acquired, such as protohypsodonty, and the

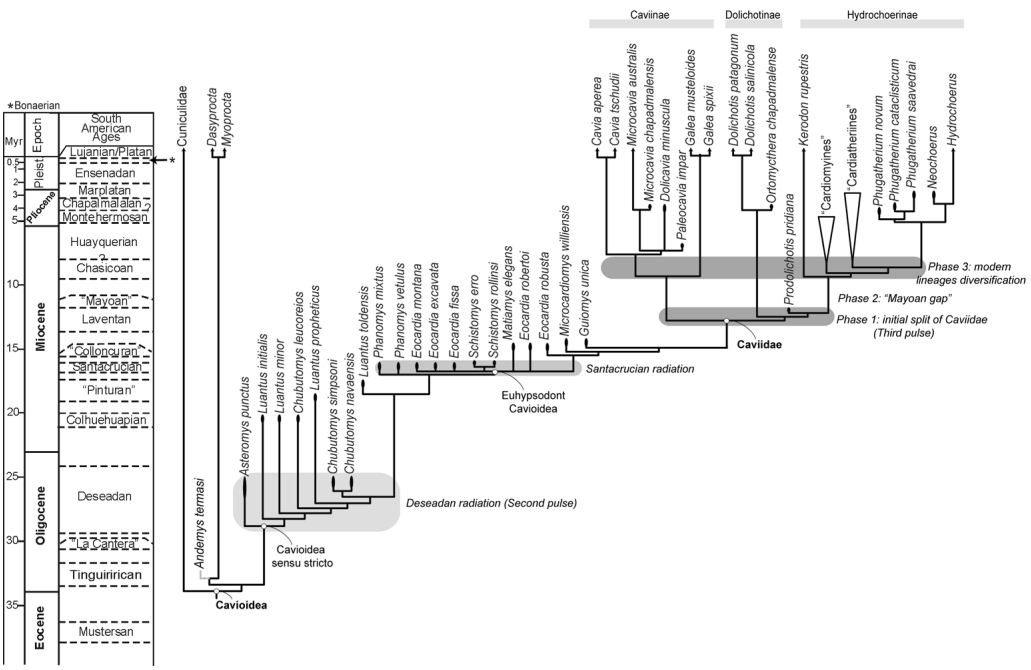


Figure 7. Evolutionary hypothesis of Cavioidea based on phylogenetic analyses of Pérez (2010a, b) and Vucetich *et al*. (2014a).

absence of the mesofossettid in lower cheek teeth in early ontogenetic stages, among other dental modifications. This first radiation of Cavioidea *s.s*. matches with that of Octodontoidea in Patagonia (second pulse of diversification= first Patagonian diversification, *sensu* Arnal and Vucetich, in press; Figs. 5, 7). During the Santacrucian (early Miocene) a second radiation of Cavioidea *s.s*. is recognized, evidenced by the record of seven species and the presence of three ghost lineages leading to "Colloncuran" forms and to the lineage that gave origin to the family Caviidae. The exceptional Santacrucian record and the sudden appearance of a high diversity of Cavioidea *s.s*. could be capturing the early offshoots of a major radiation, characterized by the acquisition of euhypsodonty, which is among the most important evolutionary novelties of the group (Pérez and Pol, 2012). Within Cavioidea, euhypsodonty is acquired only in Cavioidea *s.s*. This dental innovation must have been related to the adaptation to the main climatic-environmental changes recorded in Patagonia during the early Miocene (including great volcanic activity linked to the uplift of the Andes, a change toward more arid and colder biomes, and a general drop in humidity and temperature, etc.; Vizcaíno *et al*., 2012b). The third radiation is the diversification of Caviidae (Pérez and Pol, 2012) that must have occurred at least at 12 Ma (initial split of Caviidae, named phase 1 in this radiation) with the appearance during the Chasicoan SALMA (phase 3; about 9 Ma) of the three modern lineages Caviinae, Dolichotinae, and Hydrochoerinae, which were already highly different in their anatomy, dentition, body size, and probably even in gregarious habits (Fig. 7).

Thus, the middle Miocene represents a significant period in the evolution of caviomorphs. An important extinction of several old lineages occurred, with the rate of extinctions largely surpassing that of first appearances at the genus level (Fig. 8; App. 1). The differentiation of several modern lineages (hydrochoerines, dolichotines, dinomyids, abrocomids) found for the first time in the late Miocene is not reflected in the middle Miocene probably because of the very poor record in the late middle Miocene, known as the "Mayoan gap" (phase 2 within the third radiation of Cavioidea *s.s.*; Fig. 7; Pérez and Pol, 2012). The late Miocene also witnessed the diversification of other modern lineages (eumysopines, octodontids, ctenomyids). No other period of such important turnover has been detected (compare Figs. 5-8).

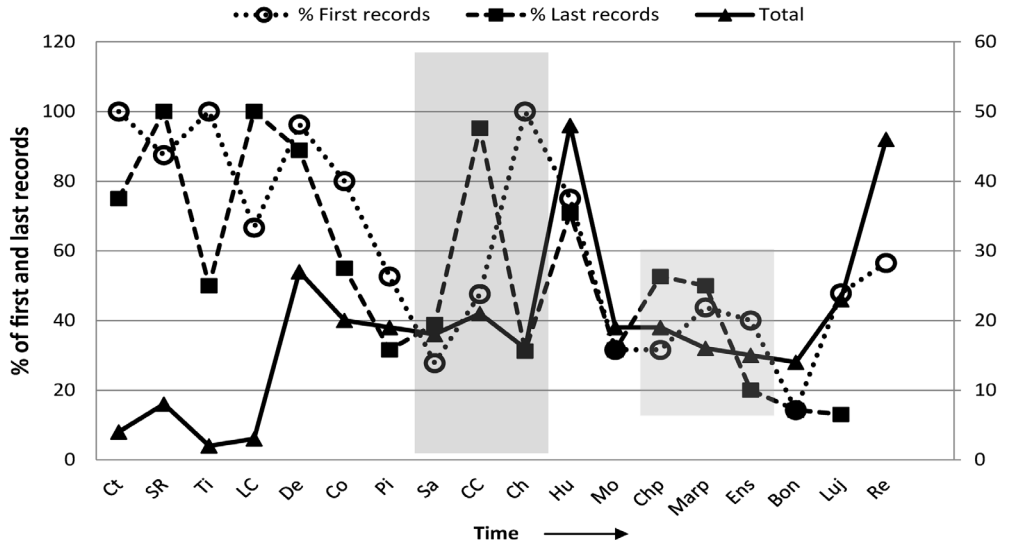


Figure 8. Percentages of first and last records of caviomorph genera through time. Gray areas show major turnover periods. Abbreviations for SALMAs and localities: **Bon**, Bonaerian; **CC**, "Colloncuran"; **Ch**, Chasicoan; **Chp**, Chapadmalalan; **Co**, Colhuehuapian; **Ct**, Contamana; **De**, Deseadan; **Ens**, Ensenadan; **Hu**, Huayquerian; **LC**, La Cantera; **Luj**, Lujanian; **Marp**, Marplatan; **Mo**, Montehermosan; **Pi**, "Pinturan"; **Re**, Recent; **Sa**, Santacrucian; **SR**, Santa Rosa; **Ti**, Tinguiririan.

Another important faunal change, although less important than the previous one, occurred between the end of the Chapadmalalan and the begining of the Ensenadan (Fig. 8) in southern South America. As with that of the middle Miocene, it also implies a certain modernization of the caviomorph fauna. The diversity of austral caviomorphs diminished gradually with the local extinction of Brazilian lineages, especially "echimyids" and erethizontids (App. 1). The gigantic hydrochoerines, dinomyids, and neoepiblemids diminished and eventually became extinct. However, many taxa closely related to living species are recorded since this period (*e.g.*, *Lagostomus*, *Neochoerus*, *Cavia*, *Galea*, *Microcavia*, *Dolichotis*, *Ctenomys*, and *Pithanothomys*, a taxon practically indistinguishable from the living octodontine *Aconaemys*; Vucetich and Verzi, 1995; Verzi *et al.*, 2009; 2014). This pauperization was probably driven by climatic changes with a general trend to cooling and desertification.

Caviomorphs and gigantism

Living caviomorphs include several species which are very large within the context of rodents, including some around 10 kg: *e.g.*, *Lagostomus maximus* (Fig. 10.6), *Dinomys branickii* (Fig. 10.3), *Cuniculus paca*, and *Myocastor coypus* (Nowak and Paradiso, 1983), besides *Hydrochoerus hydrochaeris* (Fig. 9.6-7), the giant of the living rodents, with a body mass of about 50 kg. Among living hystricognaths, Old World porcupines also reach large sizes for rodents, with weights that may reach 30 kg (Nowak and Paradiso, 1983). This suggests that hystricognaths have, more than other groups of rodents, the capability (and/or the ecological opportunity; Losos, 2010) to increase size. Most outstanding is the fact that in the past, all caviomorph lineages excluding octodontoids developed large sizes, and even more, in two of them –chinchilloids and cavioids– gigantic sizes were reached. Gigantic fossil caviomorphs have been known since the XIX Century when several of the gigantic species were described (*e.g.*, Lund, 1839; Ameghino, 1886; Moreno, 1888), but in the last decade this issue took new impetus due to the estimation of the body masses of giant forms such as *Phoberomys pattersoni* Mones, 1980 and *Josephoartigasia monesi* Rinderknecht and Blanco, 2008 (Sánchez Villagra *et al.*, 2003 and Rinderknecht and Blanco, 2008 respectively). In order to explore the distribution and magnitude of this feature among caviomorphs, we estimated the body mass of several species that reached large sizes during the Neogene using geometric similarity with a phylogenetic modern relative of known mass (Tab. 1). Because fossil mammals are mostly known only through their dentitions, we followed Hopkins (2008) in using the length of the dental series (p4-m3 or P4-M3) as a proxy for size, a dimension that allows comparison among a greater number of species than postcranial bones. In the case of the Dinomyidae and Neoepiblemidae (chinchilloids), we used two living relatives for comparison, bearing in mind the great dispersion of values among the different methods used (*e.g.*, Rinderknecht and Blanco, 2008 *vs*. Millien and Bovy, 2010). With *Dinomys branickii* (Fig. 10.3), the single living dinomyid (and the putative closest phylogenetic relative with known body mass; Sánchez Villagra *et al.*, 2003), we obtained very large body masses, with values similar to those of Rinderknecht and Blanco (2008). Using *Lagostomus maximus* (Fig. 10.6), the largest living chinchillid, we obtained lower values, about 50% smaller than those mentioned above. With hydrochoerines we used the living capybara. In the case of those taxa with no modern representatives such as the "cardiomyines", we used the dolichotinae *Dolichotis patagonum* (Fig. 10.2) and the hydrochoerines *H. hydrochoerus* and *Kerodon rupestris* (Tab. 1).

Medium to large sizes were achieved already by at least the early Miocene (Tab. 1) in lineages as different as erethizontids, neoepiblemids, and Cavioidea *inc. sed*. (Tab. 1 and App. 1). But it was during the late Miocene–Pliocene when gigantic caviomorphs were abundant and diverse. In fact, the oldest caviomorphs over 20 kg in body mass come from the Chasicoan (Figs. 1.2.s, 2; Tab. 1), and by the latest Miocene, gigantic rodents were widely distributed across the continent.

Within Cavioidea, some Huayquerian (late Miocene) capybaras could have achieved the size of the living one, as *Cardiatherium paranense* (Ameghino, 1883) or be even larger, as *C. isseli* Rovereto, 1914 (see Deschamps *et al.*, 2013; Tab. 1). Incidentally, while the hydrochoerines increased in size during the late Miocene, caviines became smaller (M.E.P. personal observation). During the Pliocene, several species greatly surpassed the size of *H. hydrochaeris*, for example, the Montehermosan (early Pliocene of the Buenos Aires Province; Deschamps *et al.*, 2013, Vucetich

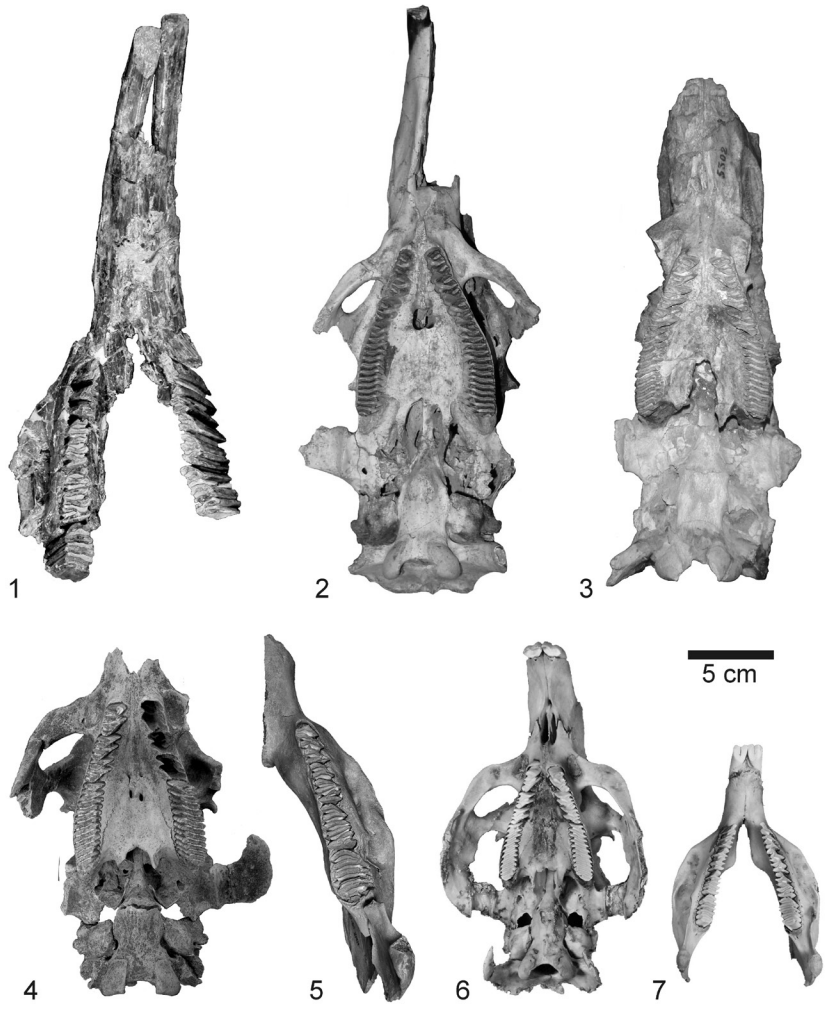


Figure 9. Gigantic hydrochoerines. 1. *Phugatherium cataclisticum*; 2. *Phugatherium novum*; 3. *Hydrochoeropsis dasseni*; 4. *Neochoerus cf. tarijensis*; 5. *Neochoerus* sp.; 6-7. *Hydrochoerus hydrochaeris*.

et al., 2014a) *Phugatherium cataclisticum,* which easily quadruples the body mass of the living capybara (Tab. 1, Fig. 9.1). The extinct "cardiomyines" also reached large size, although not as gigantic as capybaras. The largest was the Pliocene *Caviodon cuyano* Vucetich *et al.*, 2011 (Fig. 10.1), which probably greately exceeded *Dolichotis patagonum* in size (Tab. 1, Fig. 10.2).

Among Chinchilloidea, the Neoepiblemidae with *Phoberomys* Kraglievich, 1926 are among the most gigantic rodents (Fig. 10.7), and the estimation body mass in this genus has been long debated (Sánchez -Villagra *et al.*, 2003; Millien, *et al.*, 2006). Our estimations are similar to those of Sánchez Villagra *et al.* (2003), with the southern *P. burmeisteri* (Fig. 10.7) being even larger than the Venezuelan *P. pattersoni* (Tab. 1). Dinomyidae contain the greatest diversity

Table 1. Estimated body mass of some large and gigantic rodents.

Taxa	SALMA	Estimated body mass in kg	
		This paper	Previous papers
Hydrochoeridae			
Cardiatherium chasicoense	Chasicoan	12.88[a]	
Cardiatherium paranense	Huayquerian	29,55[a]	
Cardiatherium isselii	Huayquerian	90.58[a]	
Phugatherium cataclisticum	Montehermosan	238.9[a]	
Phugatherium novum	Chapalmalalan	115[a]	200 (1)
Hydrohoeropsis dasseni	post Chapalmalalan	93.68[a]	
Neochoerus	Ensenadan-Lujanian	195 [a]	110 (1); 200 (2)
Cardiomys sp. nov.	Chasicoan	4.2[a] -10.68[b] -19.97[c]	
Caviodon cuyano	Chapalmalalan?	13[a] -37.66[b] - 61.62[c]	
Cavioidea in sed.			
Neoreomys australis	Santacrucian	8.42[d]	7.12 (3)
Neoepiblemidae			
Perimys sp.	Colhuehuapian	8.53[e]	
Phoberomys burmeisteri	Huayquerian	811.65[e] - 551[f]	
Phoberomys pattersoni	Huayquerian	654.85[e] - 444[f]	437-741 (6); 220-340 (7); 200-300 (8)
Dinomyidae			
Carlesia cf. *pendolai*	Chasicoan-Huayquerian	182[e] - 111.63[f]	
Eumegamysops praependens	Huayquerian	469.7[e] - 286[f]	
Eumegamys paranensis	Huayquerian	278.6[e] – 170[f]	
Potamarchus murinus	Huayquerian	18.99[e] – 12.9[f]	
Arazamys castiglionii	Huayquerian	455.83[e] - 309.4[f]	
Isostylomys laurillardi	Huayquerian	104[e] - 70.56[f]	
Telicomys giganteus	Montehermosan	137.5[e] - 93.24[f]	
Telicomys gigantissimus	Chapalmalalan	222.98[e] -136.2[f]	
Josephoartigasia monesi	Plio-Pleistocene	917.63[e] -622.78[f]	350 (4); 1211-2584 (5)
Erethizontidae			
Steiromys duplicatus	Santacrucian		14.17 (3)
Neosteiromys bombifrons	Huayquerian	40[g] - 58[h]	

***References.** (1) Vizcaíno *et al*., 2012a; (2) Ghizzoni, 2014; (3) Candela, Rassia and Pérez, 2012b; (4) Millien, 2008; (5) Rinderckнecht and Blanco, 2008; (6) Sánchez Villagra *et al*., 2003; (7) Millien and Bovy, 2006; (8) Hopkins, 2008. The following modern species were selected for estimating body mass using geometric similarity: [a] *Hydrochoerus hydrochaeris* (50 kg), [b] *Kerodon rupestris* (1 kg), [c] *Dolichotis patagonum* (12 kg), [d] *Dasyprocta azarae* (4 kg), [e] *Dinomys branickii* (14 kg), [f] *Lagostomus maximus* (7 kg), [g] *Coendu prehensilis* (4 kg), [h] *Hystrix cristata* (22 kg).

of gigantic rodents, the most famous of which is the Plio-Pleistocene *Josephoartigasia monesi* Rinderknecht and Blanco 2008. The body mass of *J. monesi* has also been largely debated with results ranging from 200 to 2000 kg (Millien *et al*., 2006; Hopkins, 2008; Rinderknecht and Blanco, 2008; Millien and Bovy, 2010). Many other dinomyids also reached gigantic size (Tab. 1), for example, *Carlesia pendolai*, *Telicomys gigantissimus* (Fig. 10.4) and *Eumegamysops praependens*, the latter with a skull almost the size of that of *J. monesi* (Fig. 10. 8). In fact many dinomyids exceeded 100 kg during that period. Although to a lesser degree, some Erethizontidae also achieved large sizes during this period. The skull of the Huayquerian *Neosteiromys bombifrons* Rovereto, 1914 was larger than that of *Erethizon dorsatum*, and it could have reached the size of some Old World porcupines (Tab. 1).

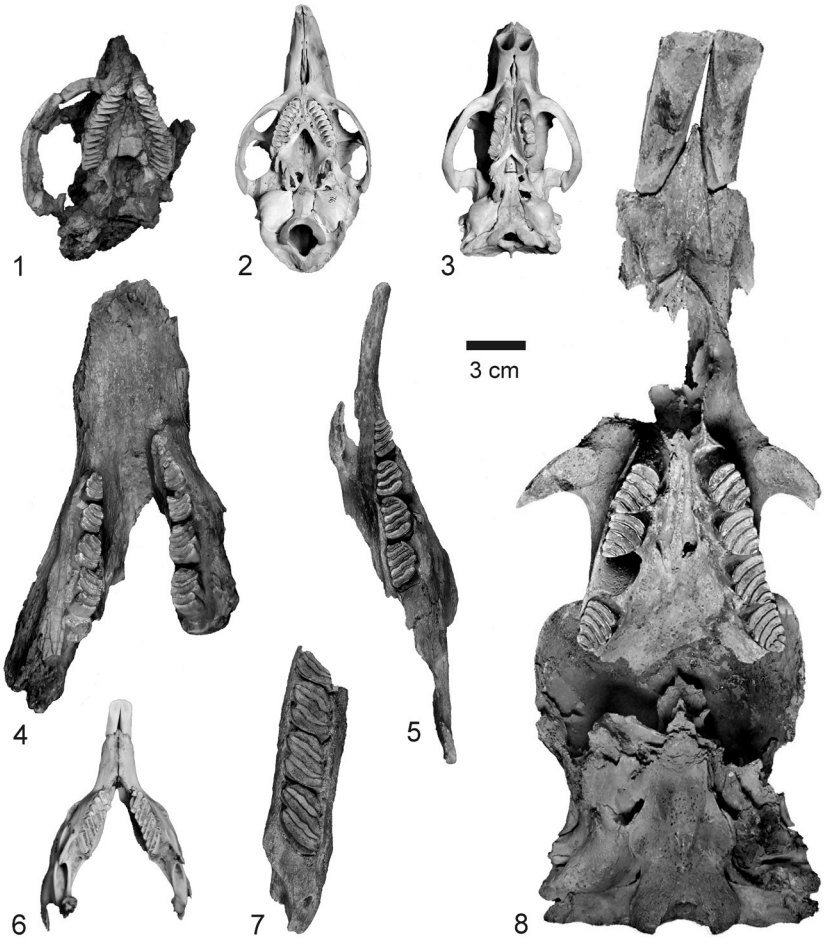


Figura 10. Large and gigantic cavioids and chinchilloids. 1. *Caviodon cuyano*; 2. *Dolichotis patagonum*; 3. *Dinomys branickii*; 4. *Telicomys gigantissimus*; 5. *Eumegamys paranensis*; 6. *Lagostomus maximus*; 7. *Phoberomys burmeisteri*; 8. *Eumegamysops praependens*.

Beyond the results of numerical estimations, some of these rodents were undoubtedly gigantic (see Figs. 9, 10). The evolution of gigantism appears as a complex issue, evolving in parallel on multiple lines, in what seems to be a coordinated phenomenon. The factors that led extinct taxa to develop such gigantic size are still under debate, but it is generally accepted that climatic change has been the driving force on evolution in size (Millien *et al*., 2006). A combination of climatic factors, mainly moisture and temperature, has been suggested as related to body size variation (James, 1970), with small body size being associated with warm and humid conditions and large size with cooler and drier conditions. Also latitudinal trends in body size have been explained as a response to temperature or water-related factors, which are predictors of primary production (Yom-Tov and Geffen, 2006). Other variables have also been proposed as important factors in the evolution of body size: basal metabolic rate, cost of transport, dominance in a community, success in mating, size and type of food, and competition (Millien *et al*., 2006 and literature therein).

In the specific case of South America, factors other than climatic change could have helped to trigger this spectacular coordinated phenomenon. On the one hand, the withdrawal of the Paranense Sea in the late Miocene allowed the development of wide plains (Pascual and Bondesio, 1982; Ortiz Jaureguizar and Cladera, 2006) represented, for example, by localities 35 and 36 in figure 2.2. On the other hand, the diversity of some large autochthonous herbivores decreased since the late Miocene (*e.g*., the Astrapotheria which became extinct during the middle Miocene, or the large toxodont notoungulates which became very rare (Bond, 1999; Vizcaino *et al*., 2012a)). It is also possible that the appearance and diversification of eutherian carnivores on the continent (Prevosti and Soibelzon, 2012) also favored the development of large sizes as a way to avoid predation.

Species richness of gigantic caviomorphs

Among gigantic rodents, several species have been recognized exclusively on the basis of differences in size. One of the paradigmatic cases is that of the numerous nominal genera and species described for the assemblages of capybaras found at a single site (Deschamps *et al*., 2007; Vucetich, *et al*., 2005a, 2014a, b). Taking an ontogenetic approach, these materials turned out to be juveniles and adults of a single species. This led to a strong reduction in the number of capybaras species. Moreover, one single species of capybaras would be present in each locality (Deschamps *et al*., 2013; Vucetich *et al*., 2014b). In the case of capybaras, the change in size is associated with a strong morphological change in molars because teeth grow allometrically (Vucetich *et al*., 2005a).

The case of eumegamyines and neoepiblemids has been less explored (but see Vucetich *et al*., 2010a). In these two groups, teeth grow isometrically, and there is not a strong morphological difference between small and large specimens. For neoepiblemids in particular, several species have been recognized both for the "conglomerado osífero" and the Urumaco Formation (Mones, 1981; Horovitz *et al*., 2005), on the basis of a few morphological differences but mainly in differences in size. However, it is reasonable to think that in each locality, specimens of different sizes represent juveniles and adults of the same species. Rinderknecht *et al*. (2011b) reached a similar conclusion for the dinomyid *Isostylomys*.

Final remarks

Caviomorph rodents have a very rich fossil record that provided a good basis for understanding the major pathways of their evolution at least in southern South America. The evolution of caviomorphs in intertropical South America is less known, although our knowledge of the Quaternary record has been improved during recent years.

The caviomorph ancestors probably entered South America during the middle Eocene by rafting from Africa, and the first steps of their evolution occurred in intertropical areas. The evidence strongly suggests that the initial radiation of caviomorphs was more complex than hitherto postulated, with the differentiation of some taxa that cannot be assigned to any of the major clades in which caviomorphs are classically divided (the superfamilies Octodontoidea, Erethizontoidea, Cavioidea, and Chinchilloidea). Caviomorphs arrived in Patagonia during the latest Eocene or early Oligocene, and by the late Oligocene they were highly diversified, with the representatives of the four main lineages being recognizable already. A large morphological disparity, at least in tooth morphology was then acquired.

The early evolution of each large clade was also more complex than previously proposed, especially for chinchilloids and pan-octodontoids. The first stages of the evolution of cavioids are more obscure because they are recognized through relatively derived Deseadan species of Cavioidea *s.s*. and because it is necessary to resolve the relationships of the middle Eocene-early Oligocene taxa proposed as Cavioidea. The steps that led to the differentiation of Dasyproctidae, Cuniculidae, and the Miocene Patagonian forms such as *Neoreomys* are not known or not well understood yet.

A better understanding of the evolutionary history of caviomorphs requires more prospecting, especially in the intertropical region, in order to recover new and more complete materials. As well, new phylogenetic analyses including a larger number of taxa will shed light on their relationships, and further paleobiological studies are necessary to understand their response to the changing environments across the Cenozoic.

Acknowledgements

We thank the editors Aldo Vassallo and Daniel Antenucci for inviting us to participate in this project. M. Reguero (Museo de La Plata), M.T. Dozo (CENPAT, Puerto Madryn) and E. Ruigómez (MEF, Trelew) graciously allowed the study of materials under their care. S. Vizcaíno kindly helped us to select a method to evaluate size. Photos of the gigantic rodents were kindly taken by B. Pianzola and P. Ungaro (MLP). We appreciate the valuable comments of the reviewer A.G. Kramarz. The project was partially supported by Grants from Agencia Nacional de Promoción Científica y Tecnologica PICTs 1115 and 2012-1483, and Universidad Nacional de La Plata N11-674.

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Appendix 1. List of South American caviomorph taxa and their temporal distribution.

Taxa	Ct	SR	Ti	"LC""	De	Co	"Pi"	Sa	CC	"EP"	LaV	"May"	Ch	Hu	Mo	Chp	Marp	Ens	Bon	Luj	Re
Cavioidea																					
"Eocardiidae"																					
Asteromys					1																
Chubutomys					1	1															
Luantus						1	1														
Phanomys							1	1													
Schistomys								1													
Eocardia								1	1												
Matiamys									1												
Microcardiodon										1											
Guiomys										1	1										

Taxa	Ct	SR	Ti	"LC""	De	Co	"Pi"	Sa	CC	"EP"	LaV	"May"	Ch	Hu	Mo	Chp	Marp	Ens	Bon	Luj	Re
Caviidae																					
Prodolichotis											1		1	1							
Allocavia													1								
Orthomyctera													1	1	1	1	1				
Pliodolichotis														1							
Palaeocavia														1	1	1	1				
Microcavia															?	1	1	1	1	1	1
Neocavia																1					
Dolicavia																1					
Dolichotis																?	1	1	1	1	1
Cavia																	1	1	1	1	1
Propediolagus																		?			
Galea																		1	1	1	1
Cardiatherium													1	1							
Phugatherium															1	1					
Hydrochoeropsis																	1				
Neochoerus																		1	1	1	
Hydrochoerus																				1	1
Xenocardia													?								
Cardiomys												1	1	1							
Caviodon														1	1	1	1				
Procardiomys													1								
Kerodon																					1
Dasyproctidae																					
Plesiaguti																			1		
Dasyprocta?														1							
Dasyprocta																					1
Myoprocta																					1
Cavioidea inc. sedis																					
cf. *Eobranisamys*	1			1																	
Eobranisamys		1																			
Eopicure		1																			
Andemys			1																		
Branisamys					1																
Australoprocta							1														

Taxa	Ct	SR	Ti	"LC""	De	Co	"Pi"	Sa	CC	"EP"	LaV	"May"	Ch	Hu	Mo	Chp	Marp	Ens	Bon	Luj	Re
Neoreomys							1	1			?										
Scleromys							1	1	1												
Megastus									1												
Olenopsis									1												
Alloiomys											1										
Mesoprocta											1										
Microscleromys											1										
Cephalomyidae																					
Cephalomys					1																
Litodontomys					1																
Cephalomyopsis					1	1															
Palmiramys					1																
Soriamys						1	1														
Banderomys						1															
Cuniculidae																					
Cuniculus																				1	1
Basal Chinchillidae																					
Loncolicu					1																
Incamys					1																
Garridomys					1																
Neoepiblemidae																					
Scotamys					1																
Perimys						1	1	1													
Phoberomys														1							
Neoepiblema														1							
Dinomyidae																					
Eusigmomys												1		?							
Simplimus												1		?							
Carlesia													1	1							
Gyriabrus													1	1							
Arazamys														1							
Diaphoromys														1	1						
Tetrastylus														1							
Eumegamys														1	1						
Tetrastylopsis														1	?						

Taxa	Ct	SR	Ti	"LC""	De	Co	"Pi"	Sa	CC	"EP"	LaV	"May"	Ch	Hu	Mo	Chp	Marp	Ens	Bon	Luj	Re
Isostylomys														1	?						
Briaromys														1							
Doellomys														1							
Potamarchus														1							
Pentastylodon														1							
Rusconia														1							
Telodontomys														1							
Pseudosigmomys														1	1	1					
Pseudopotamarchus														1							
Telicomys														1							
Eumegamysops														1							
Protomegamys																1					
Josephoartigasia																	1				
Aenigmys																		1			
"Tetrastylus"																				1	
Dinomys																					1
Chinchillidae																					
Eoviscaccia			1		1	1															
Prolagostomus							1	1	1												
Pliolagostomus								1	1												
Lagostomus													1	1	1	1	1	1	1	1	1
Lagidium																				1	1
Chinchilla																					1
Pan-Octodontoidea																					
Stem Octodontoidea																					
Eoespina	1	1																			
Eosallamys		1																			
Eosachacui		1																			
Vallehermosomys				1																	
Draconomys				1																	
Acarechimys					1	1	1	1	1		1										
Protacaremys?					1																
Deseadomys					1																
Paulacoutomys					1																
Migraveramus					1																

Taxa	Ct	SR	Ti	"LC""	De	Co	"Pi"	Sa	CC	"EP"	LaV	"May"	Ch	Hu	Mo	Chp	Marp	Ens	Bon	Luj	Re
Leucokephalos					1																
Llitum					1																
Sallamys					1																
Protacaremys						1	1	1	1												
Dudumus						1															
Willidewu						1															
Protadelphomys						1															
Caviocricetus						1															
Prospaniomys						1															
Plesiacarechimys									1												
Acaremyidae																					
Platypittamys					1																
Changquin					1																
Galileomys					1	1	1	1	1												
Acaremys						1	1	1													
Sciamys								1	1	1											
Pseudoacaremys								1	1	1											
Crown-Octodontoidea																					
Chasicomys													1								
Chasichimys													1	1							
Neophanomys														1							
aff. *Neophanomys*															1						
Myocastorinae																					
Eodelphomys		1																			
Ethelomys					1																
Xylechimys					1																
Paradelphomys						1															
Prostichomys							1														
Stichomys							1	1	1												
Spaniomys							1	1													
Adelphomys							1	1													
Paramyocastor															1	1					
Tramyocastor																	?				
Myocastor														1				1	1	1	1
Octodontidae																					

Taxa	Ct	SR	Ti	"LC""	De	Co	"Pi"	Sa	CC	"EP"	LaV	"May"	Ch	Hu	Mo	Chp	Marp	Ens	Bon	Luj	Re
Massoiamys									1	1											
Palaeoctodon													1	?	?						
Phtoramys														1	1						
Xenodontomys														1							
Pseudoplateomys														1	1						
Pithanotomys															1	1	1				
Abalosia																	1				
Aconaemys																					1
Octodon																					1
Octodontomys																					1
Octomys																					1
Tympanoctomys																		1			1
Spalacopus																					1
Actenomys															1	1	1				
Eucelophorus															1	1	1	1			
Praectenomys																?					
Ctenomys																	1	1	1	1	1
Echimyidae																					
Maruchito									1												
Gen. nov. 1									1												
Gen. nov. 2									1												
Gen. nov. 3									1												
Ricardomys											1										
Quebradahondomys											1										
Echimyidae indet.											1										
Pampamys														1							
Reigechimys														1							
Theridomysops														1							
Eumysops														?	1	1	1	1	1	1	
"E." ponderosus														1							
"E." intermedius														1							
"E." serridens														?							
"E." parodii														1							
Haplostropha														1							
Eumysopinae nov.																1					

Taxa	Ct	SR	Ti	"LC""	De	Co	"Pi"	Sa	CC	"EP"	LaV	"May"	Ch	Hu	Mo	Chp	Marp	Ens	Bon	Luj	Re
aff. *Clyomys*																			1		
Clyomys																				1	1
Euryzygomatomys																				1	1
Dicolpomys																				1	1
Callistomys																				1	1
Carterodon																				1	1
Dactylomys																				1	1
Echimys																				1	1
Thrichomys																					1
Proechimys																					1
Mesomys																					1
Hoplomys																					1
Trinomys																					1
Isothrix																					1
Lonchothrix																					1
Kannabateomys																					1
Olallamys																					1
Nelomys																					1
Toromys																					1
Pattonomys																					1
Phyllomys																					1
Abrocomidae																					
Protabrocoma													?	1	1						
Abrocoma																		1		1	1
Cuscomys																					1
Erethizontoidea																					
Erethizontidae																					
Eopululo		1																			
Protosteiromys					1																
Hypsosteiromys						1															
Eosteiromys						1	1														
Parasteiromys						1															
Branisamyopsis						1	1														
Steiromys							1	1	?		?										
Neosteiromys									?					1							

Taxa	Ct	SR	Ti	"LC""	De	Co	"Pi"	Sa	CC	"EP"	LaV	"May"	Ch	Hu	Mo	Chp	Marp	Ens	Bon	Luj	Re
Microsteiromys											1										
Paradoxomys														1							
Coendu																				1	1
Sphiggurus																					1
Chaetomys																					1
Erethizontidae?																					
Disteiromys												1									
Caviomorpha inc. sed.																					
Cachiyacuy	1																				
Canaanimys	1																				
Eoincamys		1																			
Luribayomys					1																